The economics of territory selection

Sarah N. Sells [a,*], Michael S. Mitchell [b]

[a] Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, Montana 59812, USA
[b] U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, 205 Natural Sciences Building, University of Montana, Missoula, Montana 59812, USA

ARTICLE INFO

ABSTRACT

Territorial behavior is a fundamental and conspicuous behavior within numerous species, but the mechanisms driving territory selection remain uncertain. Theory and empirical precedent indicate that many animals select territories economically to satisfy resource requirements for survival and reproduction, based on benefits of food resources and costs of competition and travel. Costs of competition may vary by competitive ability, and costs of predation risk may also drive territory selection. Habitat structure, resource requirements, conspecific density, and predator distribution and abundance are likely to further influence territorial behavior. We developed a mechanistic, spatially-explicit, individual-based model to better understand how animals select particular territories. The model was based on optimal selection of individual patches for inclusion in a territory according to their net value, i.e., benefits (food resources) minus costs (travel, competition, predation risk). Simulations produced predictions for what may be observed empirically if such optimization drives placement and characteristics of territories. Simulations consisted of sequential, iterative selection of territories by simulated animals that interacted to defend and maintain territories. Results explain why certain patterns in space use are commonly observed, and when and why these patterns may differ from the norm. For example, more clumped or abundant food resources are predicted to result, on average, in smaller territories with more overlap. Strongly different resource requirements for individuals or groups in a population will directly affect space use and are predicted to cause different responses under identical conditions. Territories are predicted to decrease in size with increasing population density, which can enable a population's density of territories to change at faster rates than their spatial distribution. Due to competition, less competitive territory-holders are generally predicted to have larger territories in order to accumulate sufficient resources, which could produce an ideal despotic distribution of territories. Interestingly, territory size is predicted to often show a curvilinear response to increases in predator densities, and territories are predicted to be larger where predators are more clumped in distribution. Predictions consistent with empirical observations provide support for optimal patch selection as a mechanism for the economical territories of animals commonly observed in nature.

1. Introduction

Territorial behavior is a fundamental and conspicuous feature observed in numerous species across diverse taxa (Adams, 2001; Brown and Orians, 1970; Burt, 1943; Maher and Lott, 2000). Territoriality occurs when an animal defends a portion of its home range (the space it uses for foraging, mating, and raising young; Burt, 1943), and is hypothesized to have evolved to protect limited resources (Brown, 1964) or young (Wolff and Peterson, 1998). For territoriality to occur, resources should be economically defendable, i.e., benefits obtained

should outweigh costs of ownership (Brown, 1964). Economic defendability may be influenced by factors related to population density and the quantity, quality, distribution, or predictability of resources (Maher and Lott, 2000).

The extent of competition for resources and their economic defendability likely help explain the range of territorial behaviors observed (Brown, 1964). Only some populations within a given species may exhibit territorial behavior if resources are not economically defendable range-wide. Although many territories are defended seasonally (e.g., during the breeding season), animals may defend territories year-round

---

if economical. Where the entire home range is economically defendable, territories may encompass most or all of the home range, as observed, e. g., for gray wolves (*Canis lupus*; Mech and Boitani, 2003), African lions (*Panthera leo*; Packer et al., 1990), white-throated magpie-jays (*Calocitta formosa*; Langen and Vehrencamp, 1998), and red-capped cardinals (*Paroaria gularis*; Eason, 1992). Conversely, animals may defend a portion of their home range if only specific resources are economically defendable (Hixon, 1980), as observed, e.g., for Hawaiian honey creepers (*Vestiaria coccinea*; Carpenter and MacMillen, 1976), rufous hummingbirds (*Selasphorus rufus*; Hixon et al., 1983), and sanderlings (*Calidris alba*; Myers et al., 1979). Many territories are held by a solitary individual or breeding pair. Group territoriality is relatively uncommon but likely influences a territory's economic defendability; e.g., larger packs of Ethiopian wolves (*Canis simensis*; Sillero-Zubiri and Macdonald, 1998) and prides of lions (Packer et al., 1990) appear more competitive in confrontations with smaller groups.

Territoriality can strongly influence population dynamics by structuring the spatial distribution of individuals. Territoriality limits the number of individuals who can use an area. Limited space for territories can influence the number of individuals who can breed (Brown, 1964), affecting reproductive rates as well as a population's social structure. In some species individuals unable to claim their own territories (e.g., due to lack of available space or adequate resources) bide time within their natal territories, affecting the spatial distribution of individuals and thus the population's social structure. For cooperative breeders, this also influences the number of helpers to the breeding pair (e.g., in gray wolves; Mech and Boitani, 2003), which can affect recruitment rates (Ausband et al., 2017). By influencing the spatial distribution of individuals, territoriality can also influence disease transmission by potentially limiting the spread of pathogens among individuals or groups (Altizer et al., 2003; Craft et al., 2011). A population's space use can furthermore affect the spatial distributions of other species, including competitors, predators, and prey (Creel et al., 2005; Fortin et al., 2005; Hebblewhite and Merrill, 2008; Kie, 1999; Proffitt et al., 2009).

1.1. Hypothesized drivers of territorial behavior

The specific mechanisms driving territory selection are widely hypothesized but poorly understood. Individuals presumably have been shaped by natural selection (Darwin, 1859) to select economical territories that maximize benefits over costs of territorial behavior (Brown, 1964; Emlen and Oring, 1977; Krebs and Kacelnik, 1991). Economical

territory selection could mean defending only enough area to provide the amount of resources necessary to survive and reproduce (Mitchell and Powell, 2004, 2007, 2012). A primary benefit of many territories is hypothesized to be exclusive access to food resources (Fig. 1; Brown, 1964; Hixon, 1980; Carpenter, 1987; Maher and Lott, 2000; Adams, 2001). The heterogeneous distribution and abundance of food resources should thus affect territory selection and resulting space use. (In other cases, primary benefits of territories can be burrows, den or nest sites, or other limiting resources; Maher and Lott, 2000.)

An individual's resource requirements can also affect territory selection (Fig. 1). Resource requirements increase with body size (Gittleman and Harvey, 1982; McNab, 1963; Tamburello et al., 2015), which in turn can vary by sex and age. Because movement to access and defend territorial space requires energy, travel costs should be a primary cost of maintaining territories (Mitchell and Powell, 2004, 2007, 2012).

Because territories partially or completely exclude conspecifics, intraspecific competition (e.g., maintaining boundary marks, signaling, fighting, or responding to resource depression) should be a primary cost of maintaining territories (Fig. 1; Brown, 1964; Hixon, 1980; Carpenter, 1987). Competition may have variable effects on territory selection at different competitor densities. Competitive ability could also influence costs of competition by causing less-competitive territory-holders to pay higher costs to compete for space when challenged by a stronger competitor.

Costs of predation risk may influence territory selection for some animals, especially where predation risk is high (Fig. 1; Sargeant et al., 1987, Whittington et al., 2005, Rich et al., 2012). When animals avoid areas associated with predators (e.g., Whittington et al., 2004, Lesmerises et al., 2012), the distribution and abundance of predators could affect how animals use space.

If these benefits and costs influence the economics of territory selection, as hypothesized, they are likely to have interacting effects. For example, low costs of competition may enable individuals to pay higher costs of travel, enabling a larger territory to be held. An increase in any one cost, however, will decrease a territory's economic value unless the territory-holder can reduce other costs or increase benefits obtained. For example, an increase in population size can lead to rapid increases in costs of competition, requiring the territory-holder to reassess its territory boundaries. These interacting effects add complexity to economical territories and merit further attention to better understand animal space use.
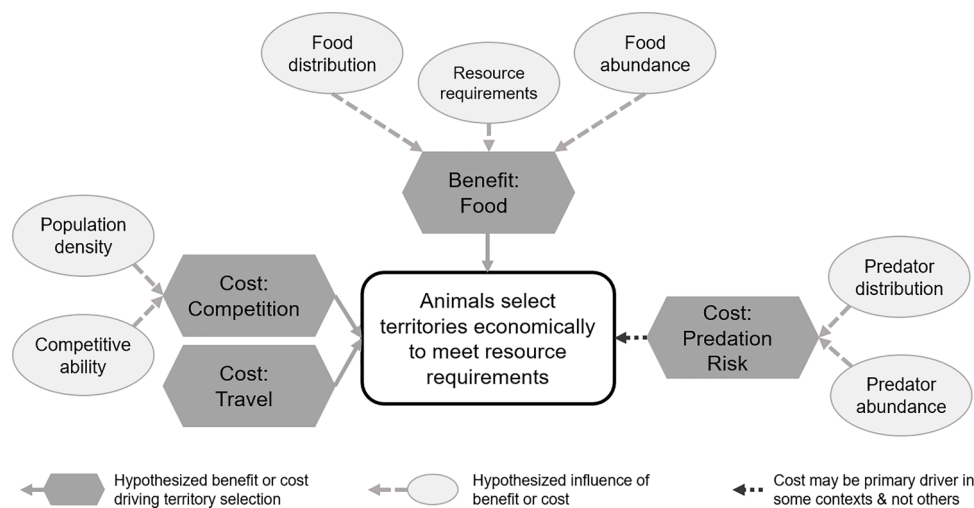

Fig. 1. Theory and empirical precedent indicate that many animals select territories economically to meet a threshold of resources for survival and reproduction, based on benefits of food and costs of competition, travel, and predation risk. These benefits and costs could be affected by numerous related considerations, as shown.
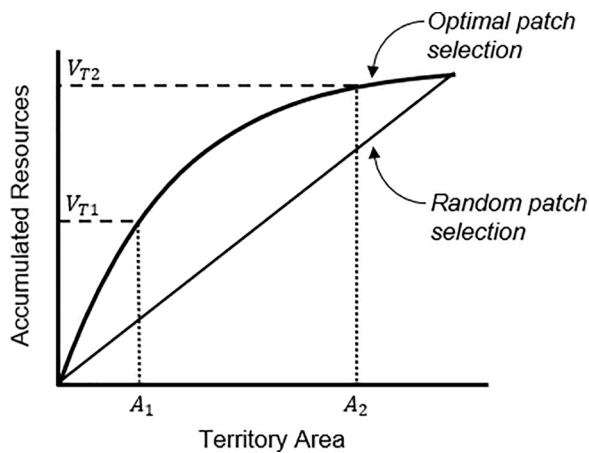
Fig. 2. Optimal patch selection for territories yields more efficient accumulation of required resources than random patch selection. By selecting territories to achieve resource requirements of V_{T1} or V_{T2}, territories will be as small as possible (i.e., area minimizing), but the territory for V_{T2} will be substantially larger (area A_1 versus A_2). Modified from Mitchell and Powell (2004).

1.2. Objectives

We sought to understand mechanisms driving territory selection. We approached this by integrating optimality models with competitor-interaction models. These two theoretical approaches to studying territoriality have largely been developed independently (Adams, 2001). Optimality models entail analyzing costs and benefits of a single territory-holder's decisions to discern fitness-maximizing rules for behavior (Adams, 2001; Krebs and Kacelnik, 1991), and produce predictions for optimal territory size (e.g., Dill 1978; Hixon et al., 1983). Optimality models generally omit explicit interactions among competitors, however, and can be difficult to test (Adams, 2001). Conversely, competitor interaction models incorporate density-dependent effects by focusing on decisions of individuals as they interact with competitors (Adams, 2001).

A model for optimal home ranges that also accounted for resource depression by conspecifics was presented by Mitchell and Powell (2004). The model was based on optimal selection of patches to include in a home range, not optimal movements; simulated animals sequentially selected patches in order of their realized value (V', equal to the resource value of a patch, V, divided by costs of regularly traveling to that patch, represented by distance, D) until reaching a threshold where adding further patches would yield no further fitness benefit. Mitchell and Powell (2007, 2012) used the model to predict optimal home ranges of telemetered black bears (*Ursus americanus*) in the Appalachian Mountains of North Carolina, USA, independent of field data collected from the bears. They found that optimal selection of home ranges to meet resource requirements in an area as small as possible (i.e., area minimization; Fig. 2) strongly predicted second order selection of home ranges (Johnson, 1980) by telemetered bears. Although this model allowed for depression of V by conspecifics, it did not more explicitly address competition by allowing agents to respond to conspecific home ranges and thus could not evaluate mechanisms of territoriality.

To understand space use of territorial animals, we developed a mechanistic, spatially-explicit individual-based model of optimal patch selection. Building on Mitchell and Powell (2004)'s foundation, we included additional costs of predation risk and competition, which we hypothesized affect territorial space use. Importantly, to understand space use of territorial animals, we added dynamic competition among competitors, where territory-holders adapted their use of space to keep it as economical as possible each time an adjacent conspecific imposed new costs of competition by contesting territory borders. We used the model to simulate territory selection for populations of animals with differing resource requirements in heterogeneous landscapes with variable food distributions and abundances, competitor densities, and predator distributions and abundances. These simulations produced empirically testable predictions for patterns in relative territory size, territory overlap, and carrying capacity, and enabled understanding the influence of individual factors and their interactions on territories of animals.

2. Methods

We developed the mechanistic model for territory selection in NetLogo 6.1.1 (Wilensky, 1999). NetLogo's graphical interface can be coded to represent simplified versions of real landscapes (Sect. 2.1) occupied by simulated animals (i.e., agents; Sect. 2.2) taking actions according to algorithms that represent the behavior of interest (e.g., territory selection; Sect. 2.3). An overview of the model follows, and Appendix A contains full details in the Overview, Design Concepts, and Details (ODD) framework of individual-based models (Grimm et al., 2006, 2010).

2.1. Simulated landscapes

We represented each landscape as a continuous grid of 200×200 patches (Fig. 3). Each patch varied by its food resources (B) and presence of predators (P). To understand the effects of variable spatial distributions and abundances of food and predators, landscapes varied in food distribution (spatial distribution of patches with high B; evenly distributed, moderately clumped, or highly clumped); food abundance (landscape-wide ΣB; low, medium, or high, and = across food distributions); predator distribution (spatial distribution of patches with high P; evenly distributed, moderately clumped, or highly clumped); and predator abundance (landscape-wide ΣP; none, low, medium, or high, and = across predator distributions, with an abundance of none representing a landscape with no predators or scenario in which costs of predation risk were unimportant to how animals selected territories).

2.2. Agents

Agents represented either individuals (for solitary species), breeding pairs (for species maintaining breeding territories), or groups (for group-living species). Agents were assigned a threshold of food resources for survival and reproduction (V_T, set to low, medium, or high; all agents received the same V_T within a given simulation). Agents were randomly assigned a competitive ability (CA_{agent}; 1 – 10, where 1 = low competitive ability and 10 = high competitive ability; equal values could alternatively be applied to all agents if desired). Each agent's objective was to maximize fitness by pursuing an economical territory. Reproduction was implicit, whereby acquiring a territory was assumed to yield reproduction opportunities.

2.3. Territory selection

For each simulation, territories and competition among agents emerged on the landscape (Fig. 4; Appendix A). At the start of each simulation, a landscape configuration and V_T was specified. A new focal agent A_i was added to the landscape and moved to an unowned patch centered in a neighborhood of patches with high value (quantified as
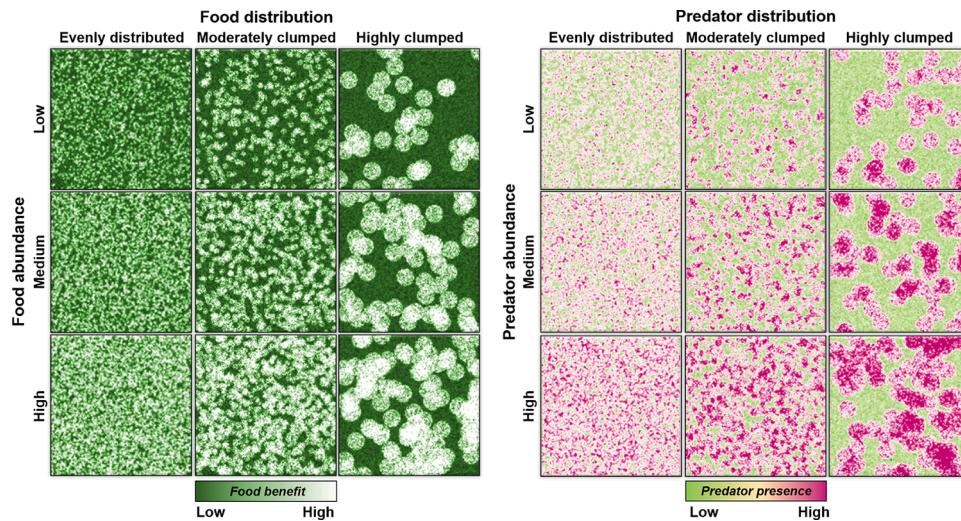
Fig. 3. Simulated landscapes were continuous grids of 200 × 200 patches. Each patch varied in benefit of food (*B*) and presence of predators (*P*). Landscapes varied in overall distribution and abundance of *B* and *P*. No two landscapes generated in the model were identical. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
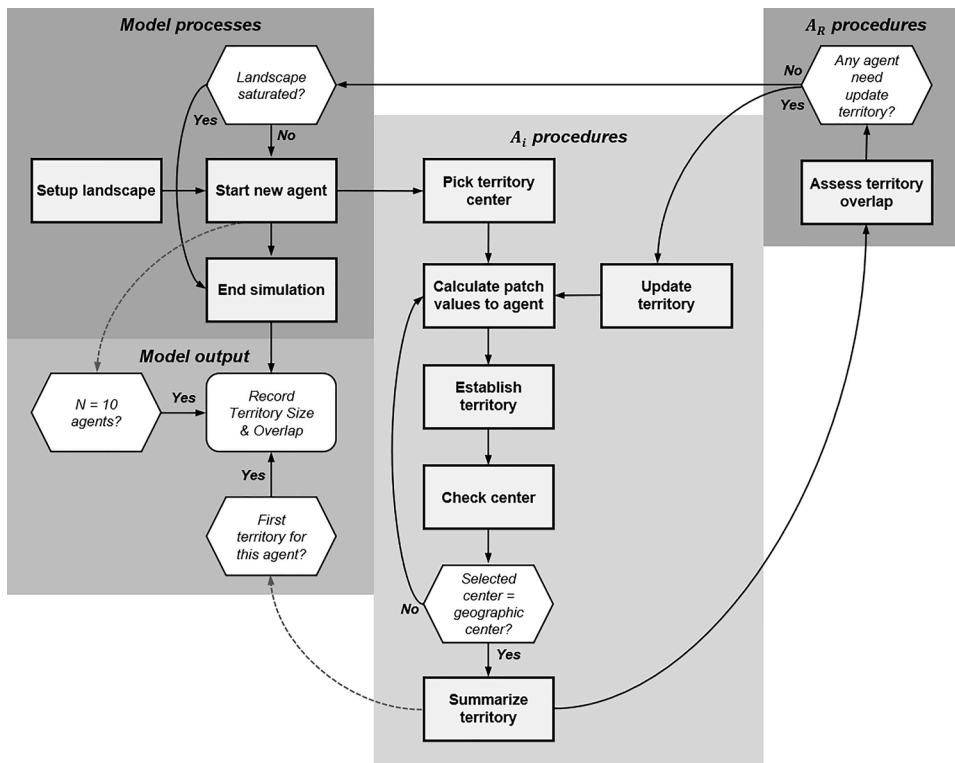

Fig. 4. The model employed a cycle of processes. After the landscape was created, an agent was added. A territory was established for the agent by identifying patches of high value. The end of the A_i procedures triggered the start of the A_R procedures of assessing overlap. If an agent's territory overlapped another or patches formerly shared were later abandoned, territories for affected agents were shifted if economical to do so. Effects of competition were thus dynamic (i.e., changed throughout the simulation) and density dependent. The number of territories gradually increased as more agents were added to the landscape. Territory summaries were collected as model output if conditions were met (gray dashed arrows indicate conditional checks). Appendix A contains full details.

having high *B* and low *P*). This patch became A_i's territory center.

The value of each patch (V_n) relative to the territory center was calculated. V_n accounted for the benefit of food (*B*) contained within patch *n*, discounted by cumulative costs of competition, travel, and predation risk to reach it from the territory center, representing the average costs that would be incurred to reach patch *n* from any patch in

the territory (Mitchell and Powell, 2004):

$$V_n = B - C_\Sigma - T_\Sigma - P_\Sigma. \tag{1}$$

C_Σ was the cumulative cost of competition. Competitors are more likely to be encountered with distance trespassed and to respond more aggressively the farther inward a trespasser intrudes (Adams, 2001;
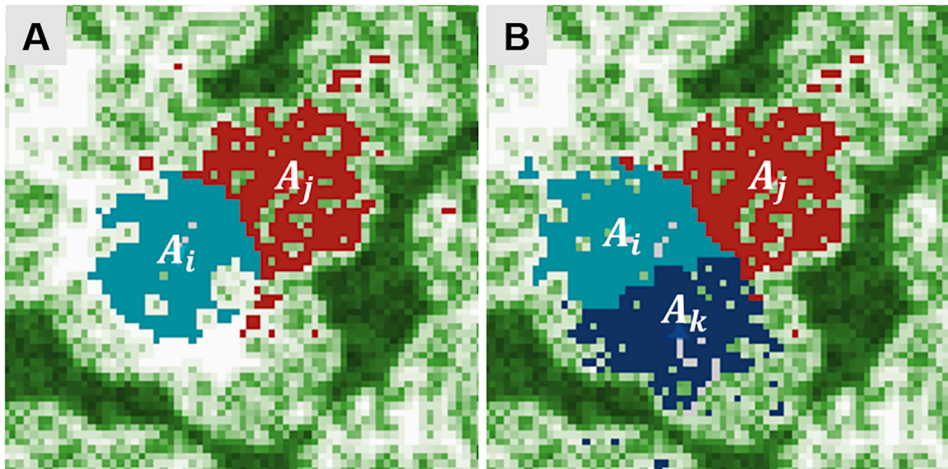
Fig. 5. Agent territories adapted to changes in competition. *Panel A*: for example, territories were selected for Agents A_i (teal) and A_j (red). *Panel B*: a territory was later selected for A_k (blue) that partially overlapped A_i's original territory. Because this overlap caused costs of competition to increase for A_i's overlapped patches, A_i's territory was shifted slightly to more economical patches. This also imposed new costs of competition along the edge of A_j's original territory, however, leading A_j's territory to shift as well. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Eason, 1992; Giraldeau and Ydenberg, 1987; McNicol and Noakes, 1981; Vines, 1979). C_Σ was therefore the sum of the local cost of competition (C_{local}) incurred by crossing each patch from A_i's territory center to patch n:

$$C_\Sigma = \sum_1^n C_{local}, \quad \text{where} \quad C_{local} = \Sigma CA_{competitor}/\Sigma(CA_{competitor} + CA_{agent}) \times C_{relative-cost}. \tag{2}$$

$CA_{competitor}$ was the competitive ability of the competing resident agent (A_R); patches had C_{local} if owned by another A_R. $C_{relative-cost}$ was set to 0.2 (Appendix B contains a sensitivity analysis). Entering patches claimed by competitors thus incurred costs proportional to the ratio of the agents' competitive abilities, even if the destination patch n was unowned. (Under equal competitive abilities, each would-be owner assumed an equal fraction of $C_{relative-cost}$.) T_Σ was the cumulative cost of travel, which accounted for D (the # of patches between the territory center and patch n):

$$T_\Sigma = D \times T_{relative-cost}. \tag{3}$$

$T_{relative-cost}$ was set to 0.01 (Appendix B). P_Σ was the cumulative cost of predation risk, which was the sum of the local cost of predation risk (P_{local}) between A_i's territory center and patch n:

$$P_\Sigma = \Sigma_1^n P_{local}, \quad \text{where} \quad P_{local} = P \times P_{relative-cost}. \tag{4}$$

$P_{relative-cost}$ was set to 0.1 (Appendix B). P_Σ meant that entering patches with predators incurred costs of predation risk, regardless of whether predators were present in the destination patch n.

After determining patch values, patches were added to A_i's territory in order of V_n until $\Sigma V_n \geq V_T$. A_i's territory consisted of selected patches (patches selected for the territory to satisfy V_T) and travel corridors (patches used to reach selected patches from the territory center, but not selected to satisfy V_T). The territory center was then assessed. If A_i's selected territory center $\neq$ the territory's geographic center (i.e., $\bar{x}$ and $\bar{y}$ coordinates of A_i's patches), A_i's current territory was discarded, A_i was repositioned to this geographic center, patch values were recalculated, and a new territory was selected. Once the territory center = its geographic center, we summarized A_i's # of selected patches, territory size (# of patches selected + # of travel corridors), territory overlap (percentage of the territory overlapped by other territories), total resources acquired (ΣV_n), and initial competitor density (ΣA_R at territory establishment).

Each A_R next determined if there was overlap with neighbors for selected patches. If yes, the A_R's territory was shifted if patches formerly selected had become uneconomical or patches formerly ignored had become economical (e.g., due to less competition for those patches;

Fig. 5). Effects of competition were thus dynamic (i.e., changing continuously throughout a simulation) and density dependent. Once all territories were shifted as needed to maintain economical territories, a new A_i was added to the landscape if sufficient resources remained for additional agents to form territories. Once the landscape was saturated (e.g., Fig. 6), the simulation ended.

2.4. Simulation experiments and analyses

We conducted simulation experiments to generate data for summarizing effects of food, resource requirements, competition, competitive ability, and predation risk on territorial space use. We completed 25 simulations for each combination of input variable for landscape (e.g., Fig. 3) and resource requirements (100, 300, and 500 to represent low, medium, and high requirements), totaling 8100 simulations. Conducting 25 simulations per combination captured variability in results. We collected output summaries for each territory formed after initial establishment, at a low population density (once 10 territories were formed), and after carrying capacity was reached (i.e., A_i could not successfully build more territories, representing a high population density). We recorded for each A_R its final territory size, territory overlap, number of nearby competitors (# of other A_R territory centers $\leq$ 25 patches from the agent's territory border), and predator density encountered (mean predator presence per territory patch). We recorded the total abundance of territories as the landscape's carrying capacity.

We used program R Version 4.0.2 (R Core Team, 2020) and packages dplyr (Wickham et al., 2019), ggplot2 (Wickham, 2016), cowplot (Wilke, 2019), and egg (Auguie, 2019) to summarize and display mean number of selected patches, territory size, and territory overlap as a function of food distribution, food abundance, resource requirements, and population density. We also summarized mean final territory size and overlap by number of nearby competitors, initial competitor density, competitive ability, predator density, and predator distribution. We scaled each agent's number of nearby competitors by the agent's
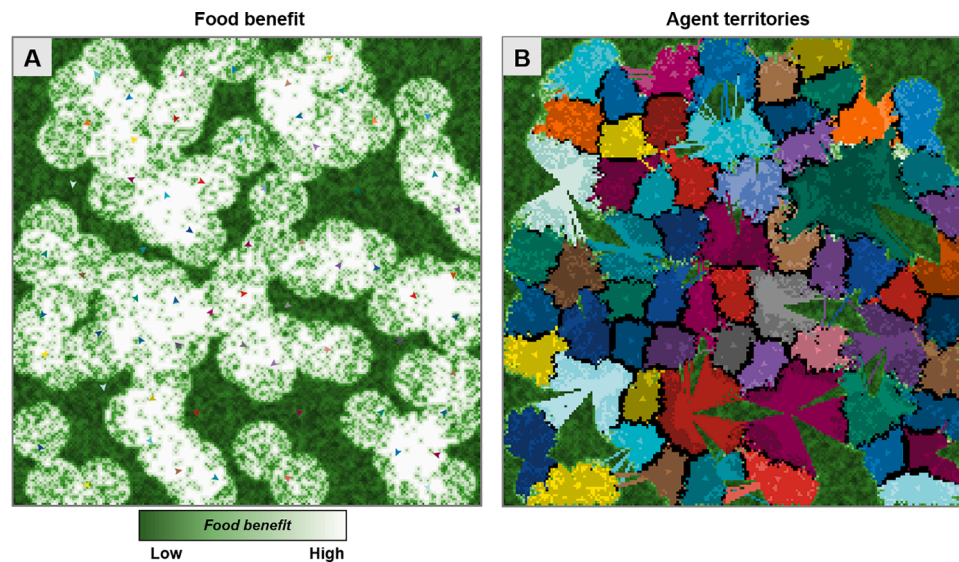
Food benefit

Agent territories

Food benefit

Low   High

Fig. 6. An example of territories formed for agents. *Panel A*: the food-benefit of patches underlying 64 agent territories (territory centers demarcated by triangles). *Panel B*: resulting territories demarcated by color. Black patches indicate territory overlap with neighbors. Mean territory size = 560 patches, range 364 – 1979.

territory size because larger territories often have more neighbors. We summarized the mean carrying capacity of each landscape. Because the importance of costs of competition, travel, and predation risk relative to one-another and benefits of food resources is unknown, we completed a sensitivity analysis with a range of potential relative costs (Appendix B).

3. Results

Agents formed > 458,000 simulated territories in total. Territories were influenced by food resources, resource requirements, competition, and predation risk, as follows.

3.1. Effects of food resources and resource requirements

Resource requirements, food distribution, and food abundance affected mean number of patches selected, territory size, territory overlap, and carrying capacity. Greater resource requirements led to greater number of selected patches, larger territories, and less overlap (Fig. 7; Table 1). More clumped or abundant food resources led to fewer selected patches and smaller territories. At high population densities, overlap was greater where food resources were more clumped. Increased food abundance led to less overlap for agents with low resource requirements, and more overlap for agents with medium or high resource requirements. Carrying capacity was higher where food resources were more clumped or abundant, and declined with increasing resource requirements (Fig. 8).

3.2. Effects of competition

Competition caused each agent's territory to change throughout the simulation as population density increased (e.g., Fig. 5). Territory size decreased and overlap increased with each additional nearby competitor (Fig. 9; Table 1). As an exception, however, when agents had low resource requirements, territories initially increased in size as the number of nearby competitors increased to low levels. The competitor density an agent encountered at territory establishment also influenced its territory size and overlap (Fig. 10). Although nearly all territories compressed from initial sizes as competition increased, territories first established at low levels of competition where food resources were highly clumped slightly expanded instead. The same was true where food resources were moderately clumped if agents had low resource requirements.

Average territory size and number of patches selected slightly changed as population density increased from low to high in any given landscape (Fig. 7; Table 1). At high population densities, mean number of selected patches was often slightly greater. Mean territory size at high population densities was slightly greater if food resources were highly clumped, but smaller if food resources were evenly distributed.

Territory size and overlap varied by competitive ability (Fig. 11; Table 1). Greater competitive ability led to smaller territories where food resources were moderately or highly clumped, and had a limited effect where food resources were evenly distributed. Greater competitive ability led to less overlap when agents had high resource requirements. The same was true for agents with medium resource requirements unless food resources were highly clumped. For agents with low resource requirements, overlap increased with competitive ability except where food resources were evenly distributed.

3.3. Effects of predation risk

Territory size often increased and then decreased curvilinearly with an increase in mean density of predators in the territory (Fig. 12; Table 1). This relationship was more linear, however, if food resources were evenly distributed or moderately clumped while predators were highly clumped. At comparable predator densities, territories were on average larger where predators were more clumped in distribution. Overlap had nuanced and variable relationships with predator distribution, and this relationship interacted with the distribution of food resources encountered. Carrying capacity declined as predator abundance increased (Fig. 8).

3.4. Sensitivity analyses

In assessing patch values for agents, we used low values for the relative costs of competition, travel, and predation risk ($C_{relative-cost}$, $T_{relative-cost}$, and $P_{relative-cost}$). This decision had limited effects on the model's predictions (Appendix B). The main effect of increasing these values was to reduce and then eliminate overlap among territories. Additionally, higher relative costs of travel and predation risk prevented agents with higher resource requirements from forming territories. Higher relative costs also increasingly eliminated differences in territory size among variable competitive abilities.
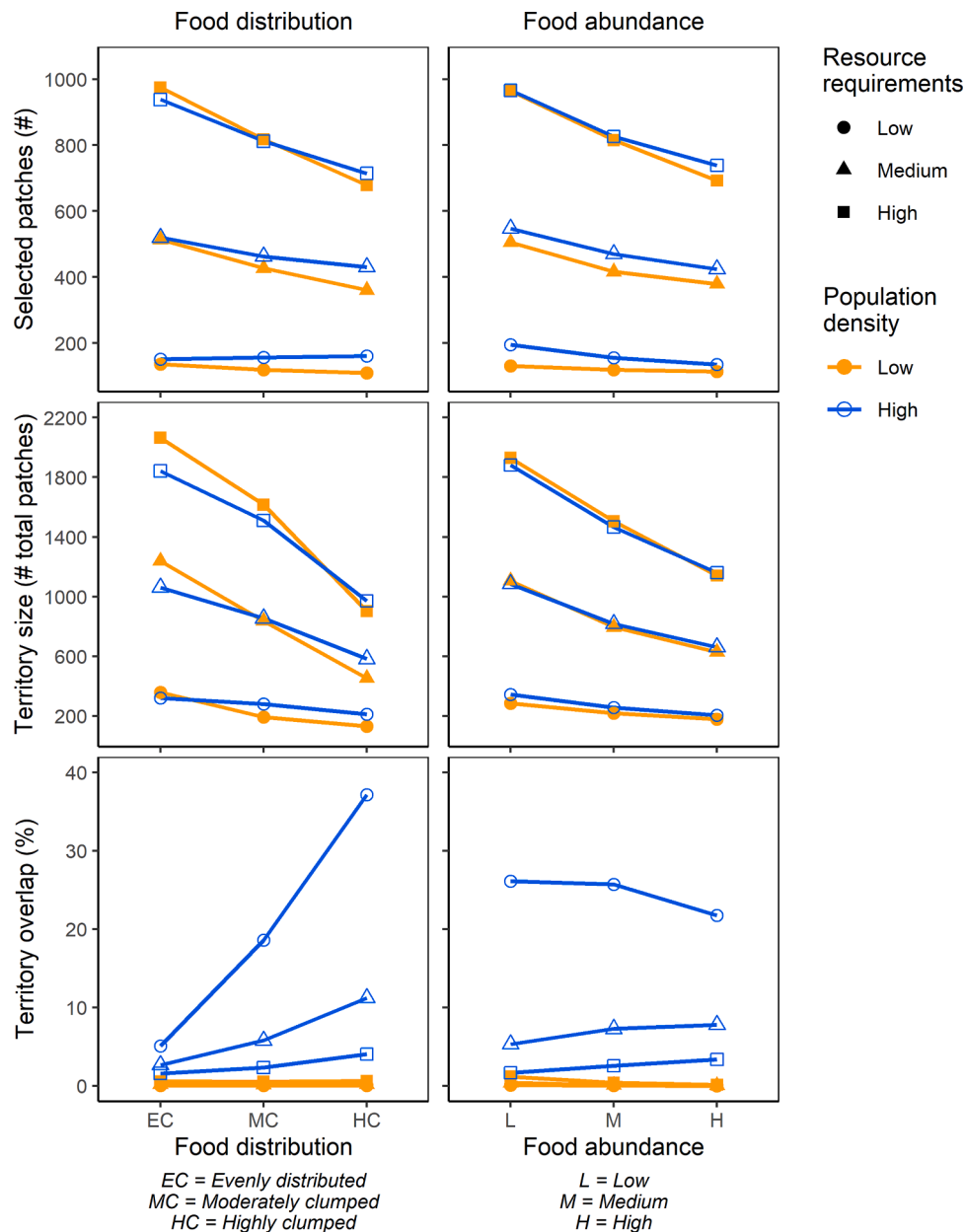
Fig. 7. Average number of selected patches (patches selected for their economic value), territory size (# of selected patches + travel corridors to selected patches), and territory overlap (percentage of the territory overlapped by other territories) varied by food distribution, food abundance, resource requirements, and population density.

4. Discussion

We developed a mechanistic, spatially-explicit individual-based model to better understand mechanisms hypothesized to drive territory selection. The model differed from existing mechanistic territory models by blending optimality and competitor-interaction approaches to selecting patches for inclusion in a territory (second order selection; Johnson, 1980), rather than modeling third-order animal movements (as demonstrated, e.g., by Lewis and Murray, 1993; White et al., 1996; Moorcroft et al., 1999, 2006; Giuggioli et al., 2011; Potts and Lewis, 2014). Our model was based on a single decision rule (do or do not select a patch based on its benefits and costs) and produced spatially-explicit predictions for territory location, size, overlap, and carrying capacity. Model simulations conducted across a broad range of landscape conditions and using no field data produced predictions. These predictions specify what may be observed empirically if the hypotheses explicit in

our model explain selection of territories and how this process structures spatial distributions and carrying capacities on different landscapes.

4.1. Clumped and abundant food resources yield smaller territories

If animals select territories economically based in part on benefits of food resources, territories are predicted to be smaller and generally have more overlap with neighbors where food resources are more clumped or abundant (Fig. 7; Table 1). More clumped or abundant food resources provide economical territory sites by offering more resources close-by, minimizing travel costs and enabling acquisition of sufficient resources in smaller territories. As vacant space becomes sparse, competitors are likely to be attracted to these same clumped or abundant food resources, yielding high densities of small, overlapping territories. This interaction of patch selection with landscape characteristics is predicted to cause carrying capacity to be greater in areas with more

Table 1.
Model predictions for mean territory size, overlap, and carrying capacity.

Scenario	Territory size	Overlap	Carrying capacity	Figures
As food distribution > clumped	−	+	+	7 – 8
As food abundance ↑	−	−or +[a]	+	7 – 8
As resource requirements ↑	+	−	−	7 – 8
As population density ↑, Δ in population mean	− or +[a]	+	NA	7
As # neighbors ↑	−[a]	+	NA	9
As competitor density ↑, Δ in individual territory	primarily −[b]	+	NA	7 & 10
Less competitive individuals or groups	+[a]	− or +[a]	NA	11
As predator distribution > clumped	+	variable[c]	NA	12
As predator density ↑	− or +[c]	variable[c]	−	8 & 12

Mean territory size = # of patches selected + travel corridors to selected patches, mean overlap = proportion of territory claimed by > 1 agent, and mean carrying capacity = maximum # of territories landscape could support.

[a] General trend with exceptions for certain food distributions, food abundances, or resource requirements.
[b] Varied by competitor density; territory size slightly increased for some territories formed at low competitor densities.
[c] Generally varied curvilinearly by predator density (territory size) or in nuanced ways (overlap).

clumped or abundant food resources (Fig. 8). Fluctuations in a food resource can be expected to cause territory size, territory overlap, and carrying capacity of a dependent species to fluctuate in response. These patterns are consistent with those observed empirically in numerous species (Table 2), supporting the hypothesis that many animals select territories economically based in part on benefits of food resources.

When different relationships are observed between food resources and territory size (e.g., Norman and Jones, 1984), the mechanisms driving territory selection may differ from those we modeled. For example, animals may attempt to maximize the resources they obtain by defending a territory to contain as many resources as possible if this increases survival and reproductive output (Schoener, 1983; Stephens and Krebs, 1986; Krebs and Kacelnik, 1991). No relationship between food resources and territory size is expected where territoriality functions to defend non-food resources such as water or denning sites (Macdonald and Johnson, 2015), mates (Macdonald, 1983), or young (Wolff and Peterson, 1998). Our results may apply to these scenarios, however, if the distribution and abundance of non-food resources are similar to the food resources in our landscapes (Fig. 3). Inconsistency with our model predictions provides a rigorous platform for developing additional mechanistic hypotheses that could account for such differences (e.g., including different or additional resources such as food and den sites).

Because energetic requirements increase with body mass (McNab, 1963; Tamburello et al., 2015), numerous predictions for territorial space use are tied to body size. Larger animals are predicted to have larger territories with less overlap, and a smaller maximum population size (Figs. 7 – 11; Table 1). This pattern is well known (Table 2). Predictions also mean that in solitary, sexually dimorphic species, territory size is likely to be larger for the larger sex (Fig. 7), as has been observed (Table 2). Although males in polygynous species are commonly thought to have large territories to gain access to multiple females (Macdonald, 1983), greater resource requirements could also contribute to this pattern. Because resource requirements are also predicted to interact with effects of competition (Figs. 9 – 11), larger individuals may respond differently to competition than smaller individuals within the same species. For example, as the number of nearby competitors increases, territory size is predicted to initially increase for smaller individuals and decrease for larger individuals (Fig. 9).

A simplifying assumption of our model was that animals can determine the quality of patches when selecting territories, even when quality fluctuates temporally (e.g., due to seasonal food resources, or competitor-induced resource depression or depletion). It is expected that natural selection has shaped animals to suitably detect patch quality. If this assumption is violated, observed patterns may be more
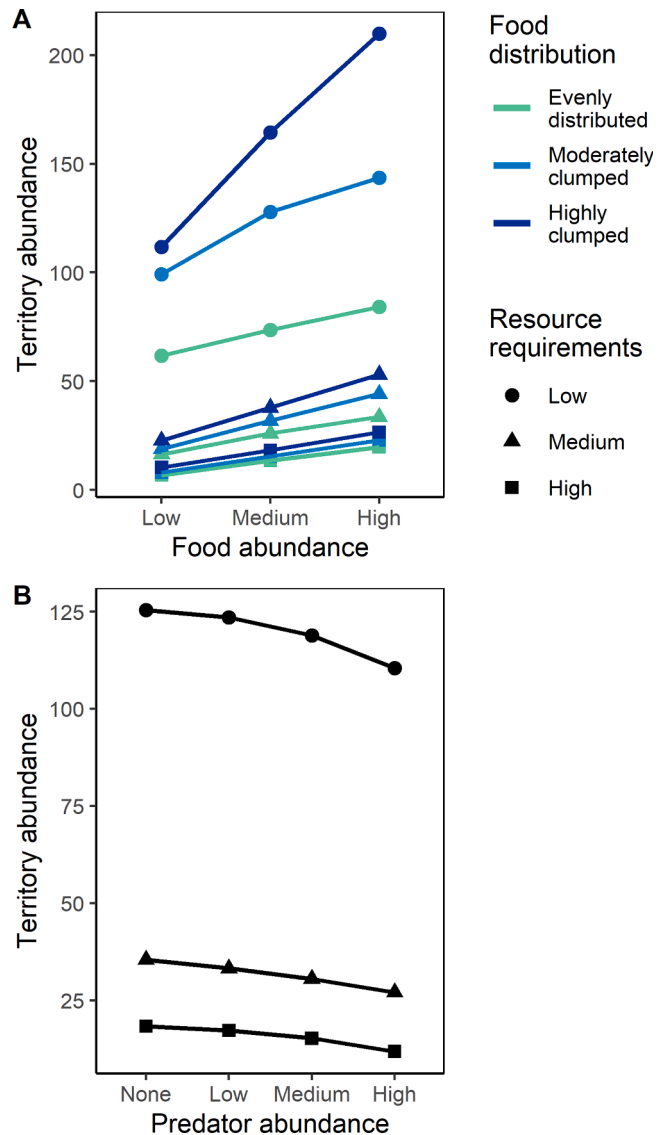

Fig. 8. Carrying capacity was affected by food distribution, food abundance, and resource requirements (*Panel A*) and by predator abundance (*Panel B*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
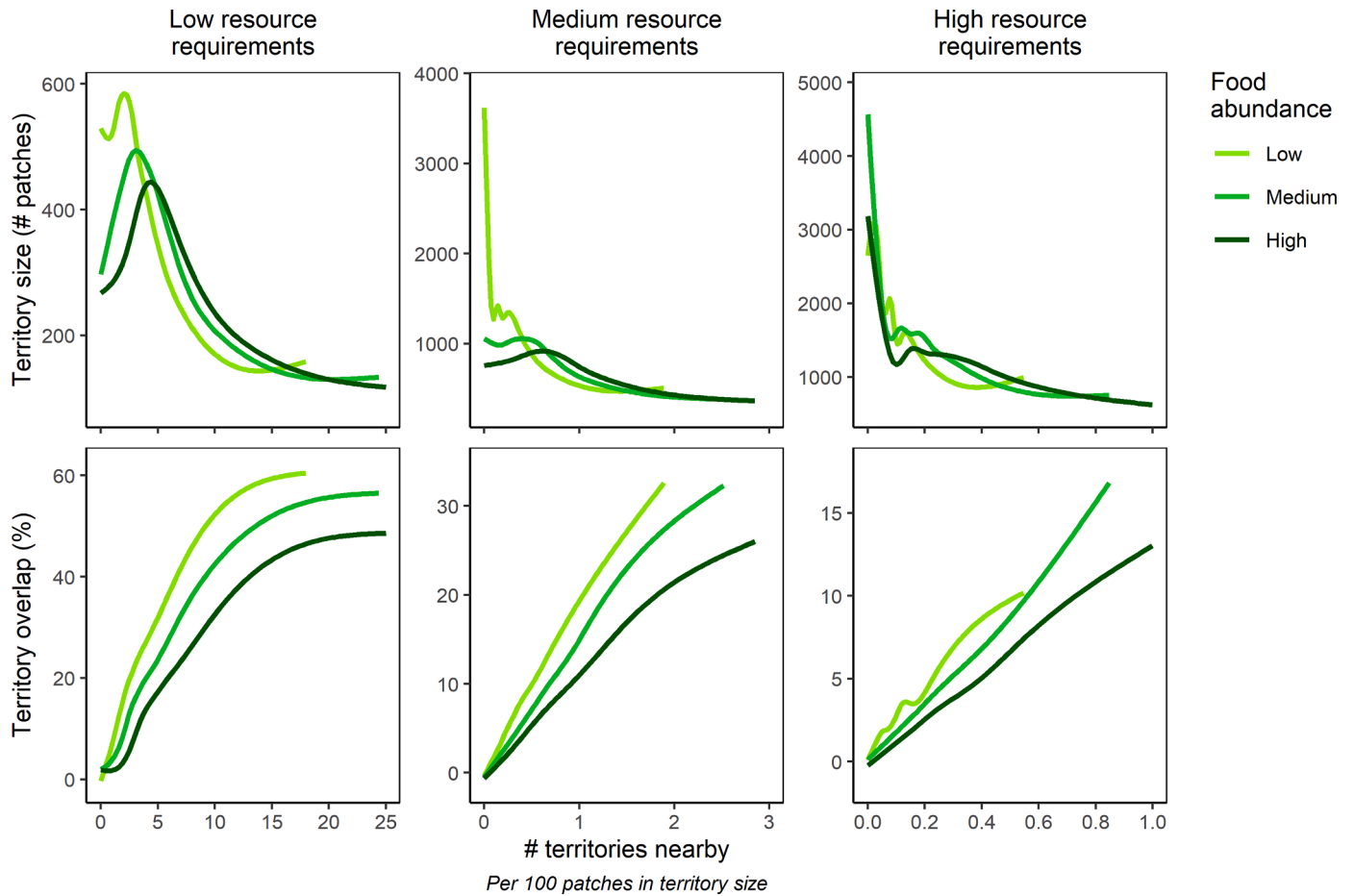
Fig. 9. Average territory size and overlap was affected by the number of nearby competitors, and the food abundance encountered. Smoothed conditional means (method = generalized additive model) are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
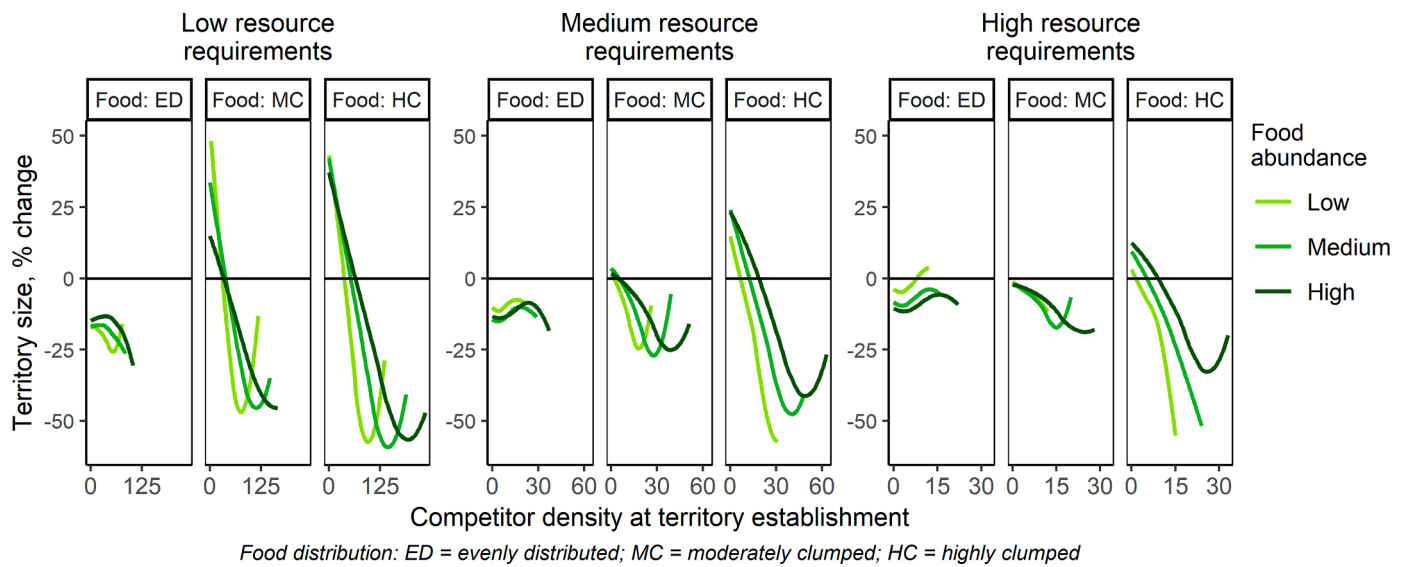

Fig. 10. Average percent change in territory size after establishment was influenced by the competitor density encountered at territory establishment, and food distribution and abundance. Smoothed conditional means (method = local polynomial regression) are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
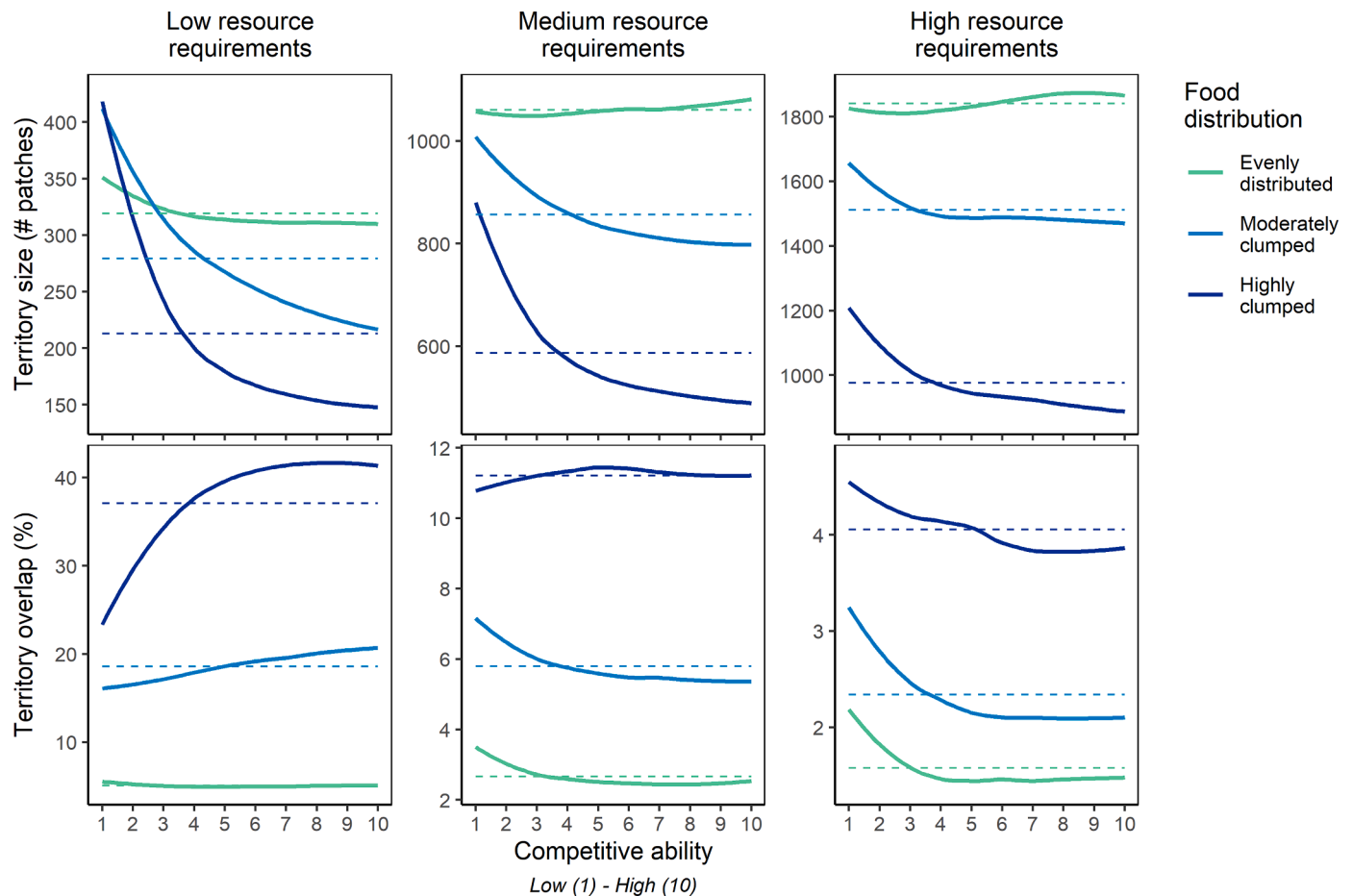
Fig. 11. Competitive ability affected territory size and overlap. Solid lines depict smoothed conditional means (method = local polynomial regression) for populations at high densities (responses varied little by competitive ability at low population densities). Dashed lines represent each mean response by food distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variable, have more outliers, or mismatch the patterns predicted by our model. Because many food benefits shift seasonally, animals that maintain year-round territories would need to select a territory to account for seasonal shifts in food or adjust seasonal territories. In such scenarios model predictions may be most applicable to seasonal patterns in territorial space use. If defense becomes uneconomical due to too-high variability in patch quality, territories may be replaced by undefended home ranges or nomadism (Powell et al., 1997; Teitelbaum and Mueller, 2019). Alternatively, resource depression or depletion alone may strongly limit overlapping space use by imposing significant costs of competition, even absent direct territorial defense (Mitchell and Powell, 2004; Spencer, 2012). Our modeling approach can be adapted to evaluate temporal changes in food abundances and resulting patch quality.

4.2. Competition generally compresses territories

As an outcome of economical territory selection, territories are predicted to compress and increase in overlap as neighboring conspecifics pose increased competition (Figs. 9 – 10). These patterns have commonly been observed empirically (Table 2), supporting the hypothesis that animals select territories economically with respect to costs of competition. Trade-offs are likely to occur as the relative economic value of patches fluctuates with competition. Low levels of one cost (e.g., competition) can enable animals to pay higher levels of another cost (e.g., travel) without changing the territory's economic value. Accordingly, when competition is low, some patches may be used primarily as travel corridors to reach more remote high-benefit patches (Mitchell and Powell, 2008). As competitors settle and impose greater costs along

territory boundaries, territory-holders will favor more proximal patches if they become more economical, causing territory compression. Compression will hit a limit, however, as territories will no longer be economical once limited resources prevent meeting minimum resource requirements. Intense competition that prohibits territories from fulfilling resource requirements would therefore lead to a breakdown of territoriality, resulting in undefended home ranges or nomadic movements instead (Powell et al., 1997; Teitelbaum and Mueller, 2019).

Some predictions for the effects of competition may seem counterintuitive. For example, where resources are more clumped in distribution, some of the first territories formed in a new population are predicted to expand as competition increases (Fig. 10). Territories selected economically at a cluster of resources will be small (Fig. 7) and unable to compress without dropping below minimum resource requirements, however, necessitating expansion as intensifying costs of competition reduce the territory's economic value. Mean territory size is also predicted to remain fairly consistent (Fig. 7) even as many territories compress with competition (Figs. 9 – 10). If animals claim areas of high economic value first, additional territories relegated to areas of lower value will be larger, yielding a relatively consistent mean territory size. Mean territory size could decline in various circumstances, however, e.g., if a very low cost of travel (such as for highly mobile species like coursing predators) enables large territories at low population densities.

Empirical estimates of a population's carrying capacity and past, current, or future population size and distribution are likely to be unreliable if trade-offs in costs and resulting outcomes in space use are ignored. Through territory compression, carrying capacity and territory
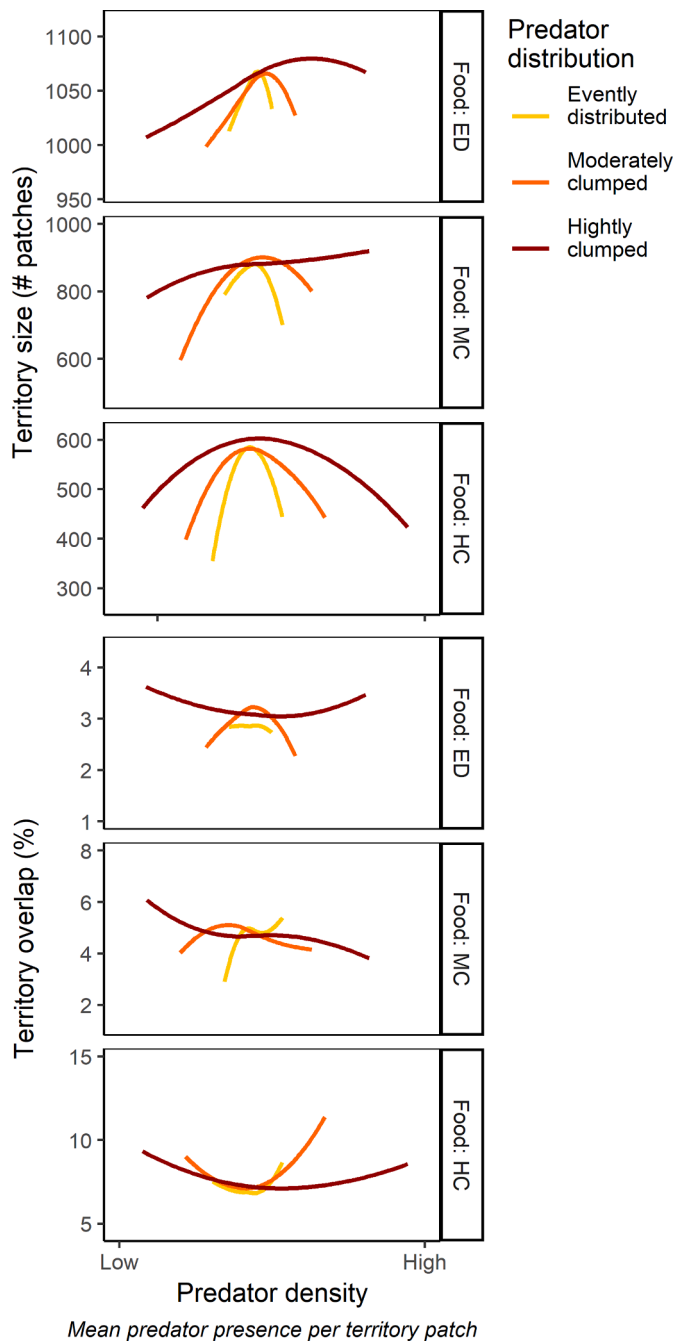
Fig. 12. Predator density affected territory size and overlap, and interacted with food distribution to produce variable effects. Smoothed conditional means (method = local polynomial regression) are shown for a medium resource requirement at medium food and predator abundances; other resource requirements, food abundances, and predator abundances had broadly similar patterns (Appendix B). For food distribution (panels), ED = evenly distributed, MC = moderately clumped, and HC = highly clumped. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

densities may reach higher levels than would be estimated using a snapshot of averaged observed territory sizes from a new or rebounding population. Likewise, territory densities would be overestimated for small populations if basing estimates on territory sizes observed at high densities. A population's estimated distribution may furthermore be relatively stable or increase at a proportionally slower rate than the number of territories as animals adjust territories in response to competition. Accordingly, a stable distribution of a population cannot be

assumed to indicate a stable population size within.

4.3. Competitive ability influences space use

If costs of competition vary inversely with competitive ability, less-competitive territory-holders are predicted to have larger territories when population density is relatively high and food resources are at least moderately clumped (Fig. 11). Unequal competitive ability can arise among dominant versus subordinate individuals, or larger versus smaller groups. Although we did not find empirical reports of how individual competitive ability affects territory size, numerous observations for social species align with our model's predictions (Table 2). Higher costs of competition may force less-competitive territory-holders to make trade-offs in space use by either acquiring larger territories to offset these costs or settling for areas of lower value to avoid competition. Although it might be assumed that dominant individuals or larger groups would have larger territories, more space does not necessarily provide more resources or greater territory quality, particularly after accounting for energetic costs of maintaining a large territory.

The combined effects of competition and the distribution of food resources could influence animal behavior and distribution (Fig. 11). Dominant territory-holders may have the greatest ability to outcompete subordinates where food resources are highly clumped given the pronounced effects of competitive ability in these areas. Social territorial species could also try to maintain larger groups to successfully compete where food resources are highly clumped. Whereas our model ceased adding new competitors once carrying capacity was reached, in real life a sufficient influx of dominant conspecifics could displace less-competitive territory-holders entirely from areas with clumped food resources. This could cause less-competitive individuals to congregate where food resources are more evenly distributed and competitive ability is predicted to have limited effects (Fig. 11), leading to sorting of individuals by competitive ability into different habitats. It could also cause less-competitive individuals to have lower fitness if pushed into less-valuable habitat, affecting demographic processes and source-sink dynamics (Pulliam, 1988).

Our assumptions that competitive ability does not correlate with resource requirements or vary over time could be modified in future iterations of the mechanistic model. If smaller individuals or groups have lower resource requirements, these less-competitive territory-holders could potentially continue to claim territories where too few resources remain available to support dominant individuals or groups, leading to an even more compact territory mosaic and greater carrying capacity than achieved in our simulations (e.g., Fig. 6). These assumptions also mean our model's predictions apply to groups with a contractionist strategy (whereby territory-holders limit group size to only what can be sustained in the territory; Loveridge et al., 2009; Macdonald and Johnson, 2015). Empirical observations of positive correlations between territory size and group size (Table 2, i.e., contrasting our model's predictions) are likely caused by an expansionist strategy (whereby territory-holders attempt to expand a territory to accommodate more group members). When resource requirements increase with competitive ability or group size, territory size should increase in response (Fig. 7).

4.4. Predators may have nonlinear effects on space use

If animals select territories economically based in part on costs of predation risk, territories are predicted to often be largest at medium predator densities (Fig. 12; Table 1). This suggests that accepting a trade-off in costs of travel enables avoiding costs of predators at medium predator densities. Trade-offs likely become uneconomical at low or higher predator densities, however, or when predators are highly clumped but food resources are not (Fig. 12). The predicted decline in carrying capacity as predator abundance increases (Fig. 8) is understandable if costs of predation risk reduces the economic value of an

Table 2
Example empirical observations in relation to model predictions.

Prediction	Example empirical observations consistent with prediction	Notes
Smaller territories with more clumped food distribution	Reported in badgers (*Meles meles*; Kruuk and Parish, 1982) and dingoes (*Canis lupus dingo*; Newsome et al., 2013).	Effects of food distribution not commonly reported
Smaller territories with greater food abundance	Numerous observations including in mollusks (e.g., Stimson, 1973); fish (e.g., Slaney and Northcote, 1974); lizards (e.g., Simon, 1975); birds (e.g., Smith and Shugart, 1987, Kesler, 2012); and mammals (e.g., Kittle et al., 2015).[1]	Many observations align with this prediction
Generally, more overlap with more clumped food distribution	Overlap was greater for dunnocks (*Prunella modularis*) where food was patchily available in time (Davies and Hartley, 1996), and for ovenbirds (*Seiurus aurocapillus*) in fragmented habitat (Mazerolle and Hobson, 2004).	Patterns in territory overlap not commonly reported[2]
Greater carrying capacity with greater food abundance	Number of rainbow trout (*Oncorhynchus mykiss*; Slaney and Northcote, 1974) and limpets (*Lottia gigantea*; Stimson 1973) increased with prey biomass. Carnivore biomass increased with prey biomass (Carbone and Gittleman, 2002). Densities of gray wolves (Fuller et al., 2003; Fuller, 1989), Ethiopian wolves (Sillero-Zubiri and Gottelli, 1995), and coyotes (*Canis latrans*; Patterson and Messier, 2001) increased with prey densities.	
Larger territories with less overlap & lower carrying capacity as resource requirements increase	Across taxa, larger-bodied animals generally require larger areas to sustain themselves (McNab, 1963; Tamburello et al., 2015). Male mink (*Mustela vison*), which are ~ twice the weight of females, maintained territories > twice the size of females territories (Yamaguchi and Macdonald, 2003).	
Smaller territories with greater competition	Reported for western gulls (*Larus occidentalis*; Ewald et al., 1980), black-chinned hummingbirds (*Archilochus alexandri*; Norton et al., 1982), sanderlings (Myers et al., 1979), anole lizards (*Anolis aeneus*; Stamps, 1990), pomacentrid reef fish (Norman and Jones, 1984), gray wolves (Rich et al., 2012), and red squirrels (*Tamiasciurus hudsonicus*; Boutin and Schweiger, 1988).	Territory size should be accounted for when evaluating the effects of competition; larger territories have greater area and thus potentially more neighbors.[3]
More overlap with greater competition	Reported for anole lizards (Stamps, 1990).	Patterns in territory overlap not commonly reported[1]
Larger territories for less-competitive individuals or groups[4] where food resources are at least moderately clumped; limited differences where evenly distributed	Observed in gray wolves (Mattisson et al., 2013; Rich et al., 2012) and dingoes (Newsome et al., 2013). Observations potentially following predictions of limited effects of evenly distributed food resources were reported for striped parrotfish (*Scarus iserti*; Clifton, 1989) and coyotes (Patterson and Messier, 2001).[5]	Conversely, territory size and group size were positively correlated in some species and variably correlated in others.[6]
Generally, curvilinearly increasing and then decreasing territory size in response to increasing predator densities	Gray wolves had larger territories where the density of humans (a primary predator) was greater (Rich et al., 2012); this aligns with model predictions if human density did not reach high levels in the wolf territories examined, or if food resources were not highly clumped.[7]	Effects of predator density rarely reported

[1] In other examples, gray wolf territory sizes increased with latitude (Mech and Boitani, 2003; Jedrzejewski et al., 2007; Mattisson et al., 2013), where productivity is generally lower (Gillman et al., 2015).

[2] Methods for delineating territory boundaries were historically often unspecified (Pyke et al., 1996), but because territories were commonly defined as the "defended area" (Maher and Lott, 1995), this may have precluded overlapping areas.

[3] E.g., Brooker and Rowley (1995) reported that territory size was positively related to the number of neighboring territories in splendid fairy-wrens, but did not control for territory size. Their finding that territory size decreased with increasing breeder density better aligns with model predictions. Mattisson et al. (2013) also reported an uncertain effect of competition on territory sizes in gray wolves, but similarly did not control for territory size.

[4] Larger groups appear to have greater competitive ability (Cassidy et al., 2015; Packer et al., 1990; Sillero-Zubiri and Macdonald, 1998).

[5] Food resources in these scenarios likely were relatively evenly distributed, as striped parrotfish fed on algae that grew abundantly throughout their territories (Clifton, 1989), and coyotes relied heavily on snowshoe hares (*Lepus americanus*, Patterson and Messier, 2001).

[6] E.g., positive correlations were reported in splendid fairy-wrens (*Malurus splendens;* Brooker and Rowley, 1995), white-throated magpie-jays (Langen and Vehrencamp, 1998), and spotted hyenas (*Crocuta crocuta*; Höner et al., 2005); variable effects were reported for lions (Loveridge et al., 2009; Mosser and Packer, 2009; Spong, 2002) and Ethiopian wolves (Sillero-Zubiri and Gottelli, 1995; Tallents et al., 2012). These apparent mismatches with our model's predictions are likely caused by an expansionist strategy, whereas our model's predictions apply to a contractionist strategy (Sect. 4.3).

[7] Because human density in this study tended to a more highly clumped distribution in urban areas, food resources also had implications on the resulting patterns (Fig. 12). Because the wolf population had not reached high levels at this time, wolves may have also successfully avoided areas with high human densities.

area. This complexity in predicted effects of predators means that a wide range of predator densities and resulting territory sizes would need to be measured; to date, such relationships appear to have been only sparsely investigated (Table 2). This deserves additional attention given opportunities to empirically measure territory size in response to a range of predator densities.

4.5. Interacting costs and benefits produce emergent effects

Many predictions reveal how interacting effects of costs and benefits produce density-dependent effects (Figs. 7 – 11; Table 1). Researchers have long sought to identify whether the effects of competition or food

most influence territory size. Our model demonstrates how these effects are unlikely mutually exclusive, and why the effects of food resources should be controlled to discern the variation in territory size attributable to competition, and vice versa (Figs. 9 – 11). Our mechanistic approach uniquely enabled understanding the interacting influences of food and competition and predicted scenarios when identical conditions will produce different effects. We suggest empirical studies continue to investigate and account for the effects of both food and competition (e. g., as demonstrated by Myers et al., 1979; Ewald et al., 1980; Norton et al., 1982; Norman and Jones, 1984), as both should be inherent to territory selection if animals select territories economically based on benefits of food resources and costs of competition.

The relative costs of competition, travel, and predation risk are unknown, almost certainly variable by species, and likely to affect a territory's overlap, economic viability, and relationship with competitive ability (Appendix B). Higher relative costs ultimately eliminated overlap among territories, suggesting that if animals select territories economically, these costs are not relatively high where territories overlap (Appendix B). Additionally, territorial behavior was no longer economical for agents with higher resource requirements at high relative costs of travel or predation risk. In species where some individuals are territorial and others are not, locally high relative costs of travel or predation risk may contribute to this flexibility in spatial behavior. Differences in territory size across competitive abilities were also increasingly eliminated as relative costs increased. Accordingly, where animals experience relatively high costs, competitive ability is not predicted to affect territory size (assuming equal resource requirements among competitors).

5. Conclusion

Our mechanistic, spatially-explicit, individual-based model aimed to increase understanding of how animals select particular territories. The model uniquely centered on optimal selection of individual patches for inclusion in a territory according to their net value, while also incorporating dynamic competition with neighboring conspecifics. Simulations produced numerous predictions for what may be observed empirically if such optimization drives placement and characteristics of territories (Figs. 7 – 12; Table 1). Our approach furthermore offers extensive opportunity for future modifications and extensions of mechanistic models for space use.

Our model can be used to predict the effects of conservation actions, thereby linking theory with conservation. In absence of data, the model provides not only predictions but a mechanistic understanding of how territorial behavior is likely to vary spatiotemporally based on numerous factors. Conservationists can use this knowledge to influence a target population's behavior and resulting distribution, abundance, and carrying capacity, e.g., by manipulating the distribution or abundance of food or predators. Such information may be particularly useful for predicting the potential success of future reintroductions and proposed conservation areas. A mechanistic understanding of how a population will respond to prey and predator distributions and abundances can furthermore help predict the effects of a species on prey populations, and vice versa. Our model can also be parameterized with empirical data to make spatially-explicit predictions (Sells, 2019), e.g., for specific locations and sizes of territories across areas of conservation concern.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109329.

References

Adams, E.S., 2001. Approaches to the study of territory size and shape. Annu. Rev. Ecol. Syst. 32, 277–303. https://doi.org/10.1146/annurev.ecolsys.32.081501.114034.

Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., Pulliam, J.R.C., 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. Annu. Rev. Ecol. Evol. Syst. 34, 517–547. https://doi.org/10.1146/annurev.ecolsys.34.030102.151725.

Auguie, B., 2019. egg: extensions for "ggplot2": custom geom, custom themes, plot alignment, labelled panels, symmetric scales, and fixed panel.

Ausband, D.E., Mitchell, M.S., Stansbury, C.R., Stenglein, J.L., Waits, L.P., 2017. Harvest and group effects on pup survival in a cooperative breeder. Proc. R. Soc. B Biol. Sci. 284, 20170580. https://doi.org/10.1098/rspb.2017.0580.

Boutin, S., Schweiger, S., 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. Can. J. Zool. 66, 2270–2274. https://doi.org/10.1139/z88-337.

Brooker, M., Rowley, I., 1995. The significance of territory size and quality in the mating strategy of the splendid fairy-wren. J. Anim. Ecol. 64, 614–627.

Brown, J.L., 1964. The evolution of diversity in avian territorial systems. Wilson Bull 76, 160–169. https://doi.org/10.1017/CBO9781107415324.004.

Brown, J.L., Orians, G.H., 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1, 239–262.

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24, 346–352.

Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. Science (80) 295, 2273–2276.

Carpenter, F.L., 1987. Food abundance and territoriality: to defend or not to defend? Am. Zool. 27, 387–399. https://doi.org/10.1093/icb/27.2.387.

Carpenter, F.L., MacMillen, R.E., 1976. Energetic cost of feeding territories in an Hawaiian honeycreeper. Oecologia 26, 213–223.

Cassidy, K.A., MacNulty, D.R., Stahler, D.R., Smith, D.W., Mech, L.D., 2015. Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. Behav. Ecol. 26, 1352–1360. https://doi.org/10.1093/beheco/arv081.

Clifton, K.E., 1989. Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behaviour. Anim. Behav. 37, 90–103. https://doi.org/10.1016/0003-3472(89)90010-9.

Craft, M.E., Volz, E., Packer, C., Meyers, L.A., 2011. Disease transmission in territorial populations: the small-world network of Serengeti lions. J. R. Soc. Interface 8, 776–786.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86, 3387–3397.

Darwin, C., 1859. On the Origin of the Species. John Murray, London.

Davies, N.B., Hartley, I.R., 1996. Food patchiness, territory overlap and social systems: an experiment with dunnocks *Prunella modularis*. J. Anim. Ecol. 65, 837–846. https://doi.org/10.2307/5681.

Dill, L.M., 1978. An energy-based model of optimal feeding-territory size 429, 396–429.

Eason, P., 1992. Optimization of territory shape in heterogenous habitat: a field study of the red-capped cardinal (*Paroaria gularis*). J. Anim. Ecol. 61, 411–424.

Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. Science (80) 197, 215–223.

Ewald, P.W., Hunt, G.L.J., Warner, M., 1980. Territory size in western gulls: importance of intrusion pressure, defense investments, and vegetation structure. Ecology 61, 80–87.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330. https://doi.org/10.1890/04-0953.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 3–41.

Fuller, T.K., Mech, L.D., Fitts-Cochran, J., 2003. Wolf population dynamics. In: Mech, L. D., Boitani, L. (Eds.), Wolves: Behavior, Ecology and Conservation. University of Chicago Press, Chicago, Illinois, pp. 161–191.

Gillman, L.N., Wright, S.D., Cusens, J., McBride, P.D., Malhi, Y., Whittaker, R.J., 2015. Latitude, productivity and species richness. Glob. Ecol. Biogeogr. 24, 107–117. https://doi.org/10.1111/geb.12245.

Giraldeau, L.-.A., Ydenberg, R., 1987. The center-edge effect: the result of a war of attrition between territorial contestants? Auk 104, 535–538.

Gittleman, J.L., Harvey, P.H., 1982. Carnivore home-range size, metabolic needs and ecology. Behav. Ecol. Sociobiol. 10, 57–63.

Giuggioli, L., Potts, J.R., Harris, S., 2011. Animal interactions and the emergence of territoriality. PLoS Comput. Biol. 7, 1–9. https://doi.org/10.1371/journal.pcbi.1002008.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and

agent-based models. Ecol. Modell. 198, 115–126. https://doi.org/10.1016/j.ec olmodel.2006.04.023.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol. Modell. 221, 2760–2768. https://doi. org/10.1016/j.ecolmodel.2010.08.019.

Hebblewhite, M., Merrill, E., 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. J. Appl. Ecol. 45, 834–844. https://doi.org/10.1111/j.1365-2664.2008.01466.x.

Hixon, M.A., 1980. Food production and competitor density as the determinants of feeding territory size. Am. Nat. 115, 510–530.

Hixon, M.A., Carpenter, F.L., Paton, D.C., 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. Am. Nat. 122, 366–391. https://doi.org/10.1086/284141.

Höner, O.P., Wachter, B., East, M.L., Runyoro, V.A., Hofer, H., 2005. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. Oikos 108, 544–554. https://doi.org/10.1111/j.0030 -1299.2005.13533.x.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Bogumiła, J., Kowalczyk, R., 2007. Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. Ecography (Cop.) 30, 66–76. https://doi.org/1 0.1111/j.2006.0906-7590, 04826.x.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61 (1), 65–71.

Kesler, D.C., 2012. Foraging habitat distributions affect territory size and shape in the Tuamotu kingfisher. Int. J. Zool. 1–7. https://doi.org/10.1155/2012/632969.

Kie, J.G., 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. J. Mammal. 80, 1114–1129.

Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., Shuter, J., Street, G.M., Thompson, I.D., Vander Vennen, L.M., Fryxell, J.M., 2015. Wolves adapt territory size, not pack size to local habitat quality. J. Anim. Ecol. 84, 1177–1186. https://doi.org/10.1111/1365-2656.12366.

Krebs, J.R., Kacelnik, A., 1991. Decision-making. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology: An Evolutionary Approach, 3rd. Oxford University Press, Oxford, United Kingdom, pp. 105–136.

Kruuk, H., Parish, T., 1982. Factors affecting population density, group size and territory size of the European badger, *Meles meles*. Journal of Zoology 1, 31–39.

Langen, T.A., Vehrencamp, S.L., 1998. Ecological factors affecting group and territory size in white-throated magpie-jays. Auk 115, 327–339.

Lesmerises, F., Dussault, C., St-Laurent, M., 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. For. Ecol. Manage. 276, 125–131. https://doi.org/10.1016/j.foreco.2012.03.025.

Lewis, M.A., Murray, J.D., 1993. Modelling territoriality and wolf-deer interactions. Nature 366, 738–740.

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., MacDonald, D.W., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography (Cop.) 32, 953–962. https://doi.org/10. 1111/j.1600-0587.2009.05745.x.

Macdonald, D.W., 1983. The ecology of carnivore social behaviour. Nature 301, 379–384. https://doi.org/10.1038/301379a0.

Macdonald, D.W., Johnson, D.D.P., 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. J. Zool. 295, 75–107. https://doi.org/ 10.1111/jzo.12202.

Maher, C.R., Lott, D.F., 2000. A review of ecological determinants of territoriality within vertebrate species. Am. Midl. Nat. 143, 1–29.

Maher, C.R., Lott, D.F., 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. Anim. Behav. 49, 1581–1597. https://doi. org/10.1016/0003-3472(95)90080-2.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G. R., Pedersen, H.C., 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173, 813–825. https://doi.org/10.1007/s00442-013-2668-x.

Mazerolle, D.F., Hobson, K.A., 2004. Territory size and overlap in male ovenbirds: contrasting a fragmented and contiguous boreal forest. Can. J. Zool. 82, 1774–1781. https://doi.org/10.1139/z04-175.

McNab, B.K., 1963. Bioenergetics and the determination of home range size. Am. Nat. 97, 133–140.

McNicol, R.E., Noakes, D.L.G., 1981. Territories and territorial defense in juvenile brook charr, *Salvelinus fontinalis* (Pisces: salmonidae). Can. J. Zool. 59, 22–28.

Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, Luigi (Eds.), Wolves: Behavior, Ecology and Conservation. University Of Chicago Press, Chicago, IL, pp. 1–34 https://doi.org/papers://A270C103-A120-4E61-B0FE-19A2B90778C5/ Paper/p4494.

Mitchell, M.S., Powell, R.A., 2012. Foraging optimally for home ranges. J. Mammal. 93, 917–928. https://doi.org/10.1644/11-MAMM-S-157.1.

Mitchell, M.S., Powell, R.A., 2008. Estimated home ranges can misrepresent habitat relationships on patchy landscapes. Ecol. Modell. 216, 409–414. https://doi.org/10 .1016/j.ecolmodel.2008.05.001.

Mitchell, M.S., Powell, R.A., 2007. Optimal use of resources structures home ranges and spatial distribution of black bears. Anim. Behav. 74, 219–230. https://doi.org/10.10 16/j.anbehav.2006.11.017.

Mitchell, M.S., Powell, R.A., 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecol. Modell. 177, 209–232. https://doi.org/10.10 16/j.ecolmodel.2004.01.015.

Moorcroft, P.R., Lewis, M.A., Crabtree, R.L., 1999. Home range analysis using a mechanistic home range model. Ecology 80, 1656–1665. https://doi. org/10.1890/0012-9658(1999)080[1656:HRAUAM]2.0.CO;2.

Moorcroft, P.R., Lewis, M.A., Crabtree, R.L., 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. Proc. R. Soc. B 273, 1651–1659. https://doi.org/10.1098/rspb.2005.3439.

Mosser, A., Packer, C., 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Anim. Behav. 78, 359–370.

Myers, J., Connors, P., Pitelka, F., 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. Auk 96, 551–561.

Newsome, T.M., Ballard, G.-A., Dickman, C.R., Fleming, P.J.S., Van De Ven, R., 2013. Home range, activity and sociality of a top predator, the dingo: a test of the resource dispersion hypothesis. Ecography (Cop.). 36, 914–925. https://doi.org/10.1111/j.1 600-0587.2013.00056.x.

Norman, M.D., Jones, G.P., 1984. Determinants of territory size in the pomacentrid reef fish, *Parma victoriae*. Oecologia 61, 60–69.

Norton, M.E., Arcese, P., Ewald, P.W., 1982. Effect of intrusion pressure on territory size in black-chinned hummingbirds (*Archilochus alexandri*). Auk 99, 761–764.

Packer, C., Scheel, D., Pusey, A.E., 1990. Why lions form groups: food is not enough. Am. Nat. 136, 1–19.

Patterson, B.R., Messier, F., 2001. Social organization and space use of coyotes in Eastern Canada relative to prey distribution and abundance. J. Mammal. 82, 463–477.

Potts, J.R., Lewis, M.A., 2014. How do animal territories form and change? Lessons from 20 years of mechanistic modelling. Proc. R. Soc. B 281, 20140231.

Powell, R.A., Zimmerman, J.W., Seaman, D.E., 1997. Ecology and Behavior of North American Black Bears: Home Ranges, Habitat, and Social Organization. Chapman & Hall, London.

Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R.A., 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. J. Wildl. Manage. 73, 345–356.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

Pyke, G.H., Christy, M., Major, R.E., 1996. Territoriality in honeyeaters: reviewing the concept and evaluating available information. Aust. J. Zool. 44, 297–317. https:// doi.org/10.1071/ZO9960297.

R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rich, L.N., Mitchell, M.S., Gude, J.A., Sime, C.A., 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. 93, 722–731. https://doi.org/10.1644/11-MAMM-A-079.2.

Sargeant, A.B., Allen, S.H., Hastings, J.O., 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51, 285–293.

Schoener, T., 1983. Simple models of optimal feeding-territory size: a reconciliation. The American Naturalist 121 (5), 608–629.

Sells, S.N., 2019. Mechanisms driving territorial and social behavior in a cooperative carnivore. Dissertation. The University of Montana, Missoula, Montana.

Sillero-Zubiri, C., Gottelli, D., 1995. Spatial organization in the Ethiopian wolf *Canis simensis*: large packs and small stable home ranges. J. Zool 237, 65–81. https://doi. org/10.1111/j.1469-7998.1995.tb02747.x.

Sillero-Zubiri, C., Macdonald, D.W., 1998. Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. J. Zool 245, 351–361. https://doi.org/10.101 7/S0952836998007134.

Simon, C.A., 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology 56, 993–998.

Slaney, P.A., Northcote, T.G., 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. J. Fish. Res. Board Canada 31, 1201–1209. https://doi.org/10.1139/f74-143.

Smith, T.M., Shugart, H.H., 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68, 695–704.

Spencer, W.D., 2012. Home ranges and the value of spatial information. J. Mammal. 93, 929–947.

Spong, G., 2002. Space use in lions, *Panthera leo*, in the Selous Game Reserve: social and ecological factors. Behav. Ecol. Sociobiol 52, 303–307.

Stamps, J.A., 1990. The Effect of contender pressure on territory size and overlap in seasonally territorial species. Am. Nat. 135, 614–632.

Stephens, D., Krebs, J., 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

Stimson, J., 1973. The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). Ecology 54, 1020–1030.

Tallents, L.A., Randall, D.A., Williams, S.D., MacDonald, D.W., 2012. Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. J. Anim. Ecol 81, 24–35. https://doi.org/10.1111/j.1365-2656.2011.01911.x.

Tamburello, N., Côté, I.M., Dulvy, N.K., 2015. Energy and the scaling of animal space use. Am. Nat. 186. https://doi.org/10.1086/682070.

Teitelbaum, C.S., Mueller, T., 2019. Beyond migration: causes and consequences of nomadic animal movements. Trends Ecol. Evol. 34, 569–581. https://doi.org/10.10 16/j.tree.2019.02.005.

Vines, G., 1979. Spatial distributions of territorial aggressiveness in oystercatchers, *Haematopus ostralegus* L. Anim. Behav 27, 300–308. https://doi.org/10.1109 /CSCWD.2007.4281399.

White, K.A.J., Lewis, M.A., Murray, J.D., 1996. A model for wolf-pack territory formation and maintenance. J. Theor. Biol. 178, 29–43. https://doi.org/10.1006/jtbi.1996. 0004.

Whittington, J., St. Clair, C.C., Mercer, G., 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecol. Appl. 15, 543–553.

Whittington, J., St. Clair, C.C., Mercer, G., 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecol. Soc. 9.

Wickham, H., 2016. ggplot2: elegant graphics for data analysis.

Wickham, H., François, R., Henry, L., Müller, K., 2019. dplyr: a grammar of data manipulation.

Wilensky, U., 1999. NetLogo.

Wilke, C.O., 2019. cowplot: streamlined plot theme and plot annotations for "ggplot2.".

Wolff, J.O., Peterson, J.a.A., 1998. An offspring-defense hypothesis for territoriality in female mammals. Ethol. Ecol. Evol. 10, 227–239. https://doi.org/10.1080/089 27014.1998.9522854.

Yamaguchi, N., MacDonald, D.W., 2003. The burden of co-occupancy: intraspecific resource competition and spacing patterns in American mink, *Mustela vison*. J. Mammal 84, 1341–1355. https://doi.org/10.1644/1545-1542(2003)084<1341: tbocir>2.0.co;2.