The economics of territory selection

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\textbf{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.

\textbf{Data accessibility} Analyses reported in this article can be reproduced using the data provided as supplementary material.

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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 sandlappers (Calidris alba; Myers et al., 1979). Many territories are held by a solitary individual or breeding pair. Group territoriality is relatively uncommon based on benefits of food and costs of competition, requiring the territory-holder to reassess its territory boundaries. These interacting effects add complexity to economical 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, Lesmess 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.

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.)

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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 (Vf, set to low, medium, or high; all agents received the same Vf within a given simulation). Agents were randomly assigned a competitive ability (CAg; 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 Vf was specified. A new focal agent Ai was added to the landscape and moved to an unowned patch centered in a neighborhood of patches with high value (quantified as

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**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).

**Logos** 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).

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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):

$$V_n = B - C \sum T \sum P \sum \zeta.$$  

(1)

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

\[
C_n = \sum_i^n C_{local}, \quad \text{where} \quad C_{local} = 2CA_{competitor}/C(A_{competitor} + CA_{agent}) \times C_{relative-cost}.
\]

\( CA_{competitor} \) 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 \( C_{relative-cost} \).) \( T_C \) was the cumulative cost of travel, which accounted for \( D \) (the \# of patches between the territory center and patch \( n \)):

\[ T_C = D \times T_{relative-cost}, \quad (3) \]

\( T_{relative-cost} \) was set to 0.01 (Appendix B). \( P_C \) 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 \( n \):

\[ P_C = \sum_i^n P_{local}, \quad \text{where} \quad P_{local} = P \times P_{relative-cost}. \]

\( P_{relative-cost} \) was set to 0.1 (Appendix B). \( P \) 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 the sum of \( V_n \) reached the territory size \( V_T \). \( A_i \)'s territory consisted of selected patches (patches selected for the territory to satisfy \( V_T \)) and travel corridors (paths 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., \( x \) and \( y \) 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 (\( \Sigma V_n \)), and initial competitor density \( (\Sigma A_R \) 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
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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

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.

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 or highly clumped, but smaller if food resources were evenly distributed. 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. 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.

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 (\(C_{\text{relative-cost}}\), \(T_{\text{relative-cost}}\), and \(P_{\text{relative-cost}}\)). 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.
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
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 (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 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).

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

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Territory size</th>
<th>Overlap</th>
<th>Carrying capacity</th>
<th>Figures</th>
</tr>
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<tbody>
<tr>
<td>As food distribution &gt; clumped</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>7 – 8</td>
</tr>
<tr>
<td>As food abundance †</td>
<td>–</td>
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<td>As resource requirements †</td>
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<td>Less competitive individuals or groups</td>
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<td>– or</td>
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<td>As predator distribution &gt; clumped</td>
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<tr>
<td>As predator density †</td>
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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.

† General trend with exceptions for certain food distributions, food abundances, or resource requirements.

* Varied by competitor density; territory size slightly increased for some territories formed at low competitor densities.

†† Generally varied curvilinearly by predator density (territory size) or in nuanced ways (overlap).

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.)
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
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
produce density-dependent effects (Figs. 7 – 11). Our mechanistic approach uniquely enabled understanding the interacting influences of food and competition and predicted scenarios when identical conditions will likely have greater area and thus potentially more neighbors.2

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., 2013). Male mink (Mustela vison), which are ~ twice the weight of females, maintained territories ~ twice the size of females at a density of 1.5 individuals/km² (Tamburello et al., 2013). Larger territories were maintained when food was patchily available in time (Davies and Hartley, 1996), and for ovenbirds (Seiurus aurocapillus) in fragmented habitat (Haxton and Hobson, 2004).

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 (Siliero-Zubiri and Gottelli, 1995), and coyotes (Canis latrans; Patterson and Messier, 2001) increased with prey densities.

Larger territories with more overlap
Many predictions reveal how interacting effects of costs and benefits produce different effects. We suggest empirical studies continue to evaluate the effects of competition; larger territories are likely to be mutually exclusive, and why the effects of food resources are not highly clumped.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 more clumped.7

1 In other examples, gray wolf territory sizes increased with latitude (Skech 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; Siliero-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 (Malarus splendens; Brooker and Rowley, 1995), white-throated magpie-jays (Langen and Vehrencamp, 1998), and spotted hyenas (Crocuta crocuta; Hörner et al., 2005); variable effects were reported for lions (Loveridge et al., 2009; Mosser and Packer, 2009; Spong, 2002) and Ethiopian wolves (Siliero-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.

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., 1985; 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 result 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.

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Supplementary materials


References

Augie, B., 2019. egg: extensions for “ggplot2”: custom geom, custom themes, plot alignment, labelled panel, symmetric scales, and fixed panel.


