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Evidence of economical territory selection in a cooperative carnivore

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As an outcome of natural selection, animals are probably adapted to select territories economically by maximizing benefits and minimizing costs of territory ownership. Theory and empirical precedent indicate that a primary benefit of many territories is exclusive access to food resources, and primary costs of defending and using space are associated with competition, travel and mortality risk. A recently developed mechanistic model for economical territory selection provided numerous empirically testable predictions. We tested these predictions using location data from grey wolves (*Canis lupus*) in Montana, USA. As predicted, territories were smaller in areas with greater densities of prey, competitors and low-use roads, and for groups of greater size. Territory size increased before decreasing curvilinearly with greater terrain ruggedness and harvest mortalities. Our study provides evidence for the economical selection of territories as a causal mechanism underlying ecological patterns observed in a cooperative carnivore. Results demonstrate how a wide range of environmental and social conditions will influence economical behaviour and resulting space use. We expect similar responses would be observed in numerous territorial species. A mechanistic approach enables understanding how and why animals select particular territories. This knowledge can be used to enhance conservation efforts and more successfully predict effects of conservation actions.

1. Background

The fundamental and conspicuous behaviour of territoriality has long been of interest to ecologists. Territoriality arises when an animal defends part or all of its home range (the area used for foraging, mating and caring for young) [1] and occurs in numerous species across diverse taxa [1–4]. Ecologists have often studied territoriality using an empirical approach; however, this generally does not provide an understanding of causal mechanisms (i.e. the underlying processes driving decisions animals make about where to settle and what to defend).

Mechanistic models provide an alternative approach to the study of territoriality. Such models aim to understand the mechanisms underlying space use and offer substantial opportunity to investigate the proximate and ultimate mechanisms driving behaviour. Mechanistic models often centre on a random walk approach [5,6]. Most models specific to territoriality build on Lewis & Murray [7], whereby partial differential equations model diffusive movement and
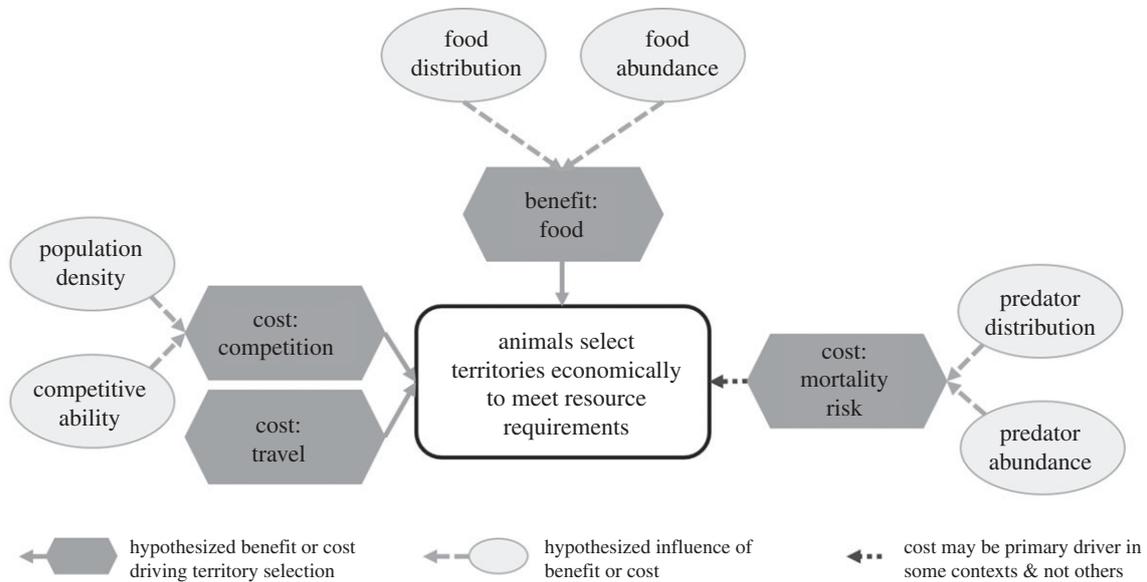
Figure 1. Hypotheses underlying the Sells & Mitchell [11] mechanistic territory model. Territories that maximize benefits and minimize costs of ownership should lead to higher fitness [12–14]. Accordingly, as a product of natural selection [15], animals are presumably adapted to select territories economically [12]. Economical territories should be only large enough to provide requisite resources for survival and reproduction, except in cases where additional resources increase fitness [8–10]. A primary benefit of many territories is probably exclusive access to food resources [2,12,16,17] because food is essential to survival and reproduction. Primary costs are probably competition [12,16,17] and travel [8–10] because the competition is inherent to territoriality and energy is needed to access and defend resources. Territory holders with lower competitive ability may pay higher costs to compete against more-competitive conspecifics [18–20]. Mortality risk may also be a primary cost if it affects how animals select and use their territory [21,22]. From Sells & Mitchell [11].

advective response towards a territory centre in response to foreign scent marks [5,6]. Optimal foraging theory has not typically been addressed within such models [5]. Using a different method centred on optimal foraging theory rather than movement, Mitchell & Powell [8] presented a novel mechanistic model of optimal patch selection for inclusion in a home range. Application of their model revealed that black bears (*Ursus americanus*) structure home ranges optimally with respect to the spatial distribution of food resources [9,10]. This model was limited to home ranges of non-territorial species, as the competition was represented implicitly through resource depression (i.e. exploitative competition) rather than explicitly simulating dynamic competition among territorial animals (exploitative and interference competition).

Building on the foundation of Mitchell & Powell [8], a recently developed mechanistic territory model [11] represented the hypothesis that animals are adapted to select territories economically (figure 1). The model was based on the optimal selection of individual patches for inclusion in a territory. As simulated populations gradually increased, simulated animals employed a behaviour rule to maintain economical territories by selecting and defending territory patches that maximized net values of ownership, represented as food benefits minus costs of defending and using the territory (costs associated with travel, competition and mortality risk). Territories were selected to meet a threshold of resource requirements as economically as possible (i.e. an area minimizing approach [8]). Territory holders continued defending and modifying their territories in response to decisions made by neighbouring competitors, allowing for interaction among conspecifics. The model produced numerous empirically testable predictions (table 1), including that greater food abundance and competitor density would lead to smaller territories. Territory size was also predicted to often vary inversely with competitive ability when population density was high, and to often increase before decreasing curvilinearly in response

to greater levels of mortality risk. A curvilinear response suggests there are increasingly economical trade-offs with other benefits and costs, such as through abandoning areas of high mortality risk and accepting higher costs of competition by overlapping other territories [11].

Alignment of the mechanistic model's predictions with reality would contribute evidence for the economical selection of territories as a causal mechanism underlying ecological patterns observed [11]. We therefore sought to determine whether the model suitably predicted and explained patterns in space use of a real population. We tested the model's predictions using grey wolves (*Canis lupus*) in Montana, USA, as a case study.

The mechanistic model's hypotheses are easily extended to wolves (table 1) [11]. This strongly territorial species maintains territories year-round [23]. Ungulates comprise the bulk of wolf diets [24,25]. Groups generally consist of a dominant breeding pair and their offspring from multiple years who cooperatively defend the territory, hunt and raise pups. Larger groups of carnivores may have the greater competitive ability [18–20] and therefore reduced costs of competition with neighbouring groups. Wolves are coursing predators who traverse long distances, and such movement is energetically costly. Following the concept of economical territories [11], areas costlier to own would necessitate more benefits to offset the cost, resulting in larger territories. For coursing predators, rugged terrain may increase travel costs [26]. It is also possible that rising travel costs eventually become uneconomical such that territory size declines curvilinearly at high levels of ruggedness, as with the predicted response to mortality risk [11]. Roads with low human use may conversely offer more efficient routes for traversing the territory [21,27–29]. Greater efficiency may increase net economic values such that less space satisfies resource requirements. Alternatively, greatly decreased costs of travel could make distant areas economical, particularly if resources are heterogeneously distributed, leading to larger territories instead.

Table 1. A mechanistic model's hypotheses and predictions for economical territory selection [11], and evidence of these patterns in territories of grey wolves. Yes = results consistent with hypothesis (90% confidence intervals [CI's] exclude 0); no = no support; CI overlaps 0.

hypothesis: animals select territories economically based on benefits and costs:	prediction for territory size[a]	variable	grey wolves: results consistent with hypothesis?
food resources are a primary benefit structuring space use	↓ where prey abundance ↑	$ungulate_{summer}$	yes
		$ungulate_{winter}$	yes
competition is a primary cost structuring space use; additionally, smaller groups pay higher costs to compete	↓ as # nearby competitors ↑	$competitor_{density}$	yes
	↓ as group size ↑ at high population densities	$group_{size}$	yes
travel is a primary cost structuring space use; in our system, rugged terrain is more costly and low-use roads are less costly	↑ where ruggedness ↑ to offset this cost	ruggedness	yes
	alternatively, n-curvilinear response to ruggedness	$ruggedness^2$	yes
	↓ where road density ↑ given lower costs[b]	$roads_{low\text{-}use}$	yes
mortality risk is a primary cost structuring space use	n-curvilinear response	$roads_{low\text{-}use}^2$	no
		$density_{humans}^2$	no
		$harvest_{mortalities}^2$	yes

[a]Predictions were provided by the Sells & Mitchell mechanistic model [11]. We focused on patterns in territory size because these are most readily measured from available data for wolves. We omitted patterns in overlap because the full territory mosaic and resulting territory overlap cannot be known (absent simultaneously deploying collars on wolves in every territory).

[b]Alternatively, if reduced travel costs on low-use roads make distant areas more valuable, territory size may instead ↑ where road density ↑. This alternative was simultaneously tested by the variable $roads_{low\text{-}use}$ and was not supported.

Mortality risk may also shape space use [11]. For wolves, humans are generally a primary source of mortality [30,31] and harvest has occurred in our study system for the past decade. Wolves are intelligent and adaptable [32] and often avoid humans [33–35]. Whether permanent or limited to specific times of day or seasons, avoidance of sites associated with higher mortality risk could necessitate expansion of the territory to maintain its economic value, until trade-offs in other costs and benefits become more economical [11]. We hypothesized that costs of mortality risk increased with density of low-use roads (which may also provide easier travel for not only wolves, but hunters, trappers and other recreationists), density of humans and greater numbers of conspecifics recently killed via harvest.

2. Study area

Our study area comprised the northern extent of the US Rocky Mountains in western Montana (figure 2). Elevations ranged 554–3938 m [36]. Northwestern Montana was rugged and mountainous, with dense forests and a climate typical of the Pacific Northwest. Rolling foothills and rugged mountains characterized southwestern Montana, where shrubs and bunchgrasses transitioned to conifers and alpine vegetation at increasing elevations. The low rolling hills and rugged mountain canyons of west-central Montana had a mix of montane forest, shrub desert, intermountain grasslands and alpine plateaus. Annual number of wolf groups verified by Montana Fish, Wildlife and Parks (MFWP) was 134 (2014), 126 (2015), 118 (2016), 124 (2017) and 129 (2018). Primary prey for wolves were elk (*Cervus canadensis*), white-tailed deer (*Odocoileus*

virginianus), mule deer (*O. hemionus*) and moose (*Alces alces*). Other large carnivores included coyotes (*C. latrans*), mountain lions (*Puma concolor*), black bears and grizzly bears (*U. arctos*). The human population in Montana was just over 1 062 000 in 2018 (census.gov). From 2014 to 2018, the harvest season for wolves occurred each 1 September–15 March and resulted in 205–259 mortalities per year by hunting and trapping.

3. Methods

(a) Wolf location data and territories

From 2014 to 2019, MFWP captured wolves using foothold traps or aerial helicopter captures to deploy global positioning system (GPS) collars. Captured wolves were fitted with GPS collars programmed to collect latitude and longitude every 3–13 h for 2–5 years (depending on collar features and expected battery life).

MFWP wolf specialists determined group membership of each collared individual. A wolf was considered a resident of its group while its movements were in a localized cluster, including limited forays, defined as departing from and returning to the cluster. We considered a wolf to no longer be a resident if it did not return to its territory, or forays became frequent (this nearly always precipitated full dispersal; frequent forays were defined as starting a new foray less than one month after returning from a previous one). Upon dispersing, the individual could either die or join a new group by again localizing its movements. Successful dispersers were identified as a member of the nearest group or given a new group identification if the cluster did not overlap a known territory centroid.

We estimated territory sizes using volume-adaptive kernel density estimates (KDEs) [37] for individuals that remained residents of groups for greater than or equal to 70% of a year (shorter
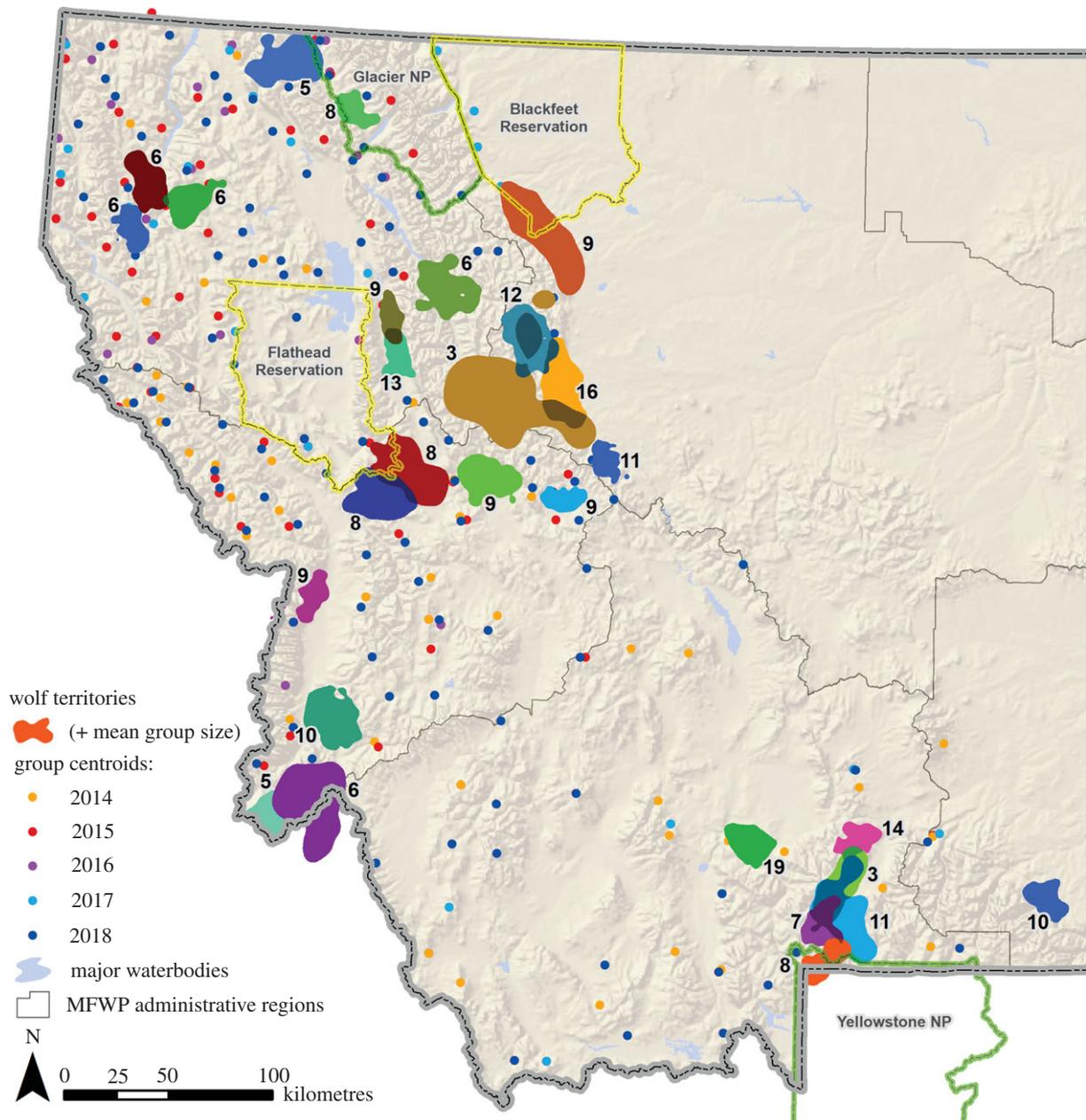
Figure 2. Locations of 28 annual territories estimated for collared wolves. Adjacent numbers were the mean group size in the 2 years post-capture. (Online version in colour.)

periods may not delineate full territories). We used R software [38] with package AdehabitatHR [39], a 95% KDE, and a smoothing parameter of 100% of the reference bandwidth. This reduced islands and lacunas while excluding extra-territorial forays, providing an estimate of territory boundaries using methods similar to past work in our study system [22] and for other large carnivores (e.g. [40–44]). For each collared individual, we generated KDEs for each sequential year. We also generated 90% KDEs to enable comparisons to past estimates of territory sizes in Montana [22]. We excluded two individuals whose territories were mostly or entirely outside of Montana (beyond which covariate data were not readily available), three individuals that appeared transient and two individuals whose collars functioned intermittently (transmitting less than 1 fix every 5 days on average).

(b) Explanatory variables

We generated explanatory variables to represent the benefit of prey resources and costs of competition, travel and mortality risk using R [38]. We represented prey resources as summer and winter ungulate density indices, competition as competitor

density and group size, travel as terrain ruggedness and low-use road densities, and mortality risk as low-use road densities, human densities, and harvest mortalities (table 1). For competitor density, group size and harvest mortality, we averaged data from the calendar year in which the collar was deployed (year T) and the following year ($T + 1$) because collars were deployed at variable times of year. We used the most recent year of data available for these variables in limited cases where data were unavailable.

We estimated ungulate densities within each KDE. In each km² grid cell i delineated as summer deer habitat (fieldguide.mt. gov), we calculated a summer deer density index as

$$\text{deer(summer)}_i = (N_R \div \Sigma_{\text{area}}) \times (\text{CPUE}_i \div \text{CPUE}_{\bar{R}}).$$

N_R was MFWP's 10-year average estimate of white-tailed and mule deer abundance in the MFWP administrative region (R) where i fell. Σ_{area} was R's estimated area of deer summer habitat. CPUE_i was the mean catch per unit effort (CPUE; male harvest/ hunter days) in the MFWP hunting district in which i fell, and $\text{CPUE}_{\bar{R}}$ was the regional mean CPUE, based on MFWP harvest records from 2008 to 2017. We repeated these calculations for a
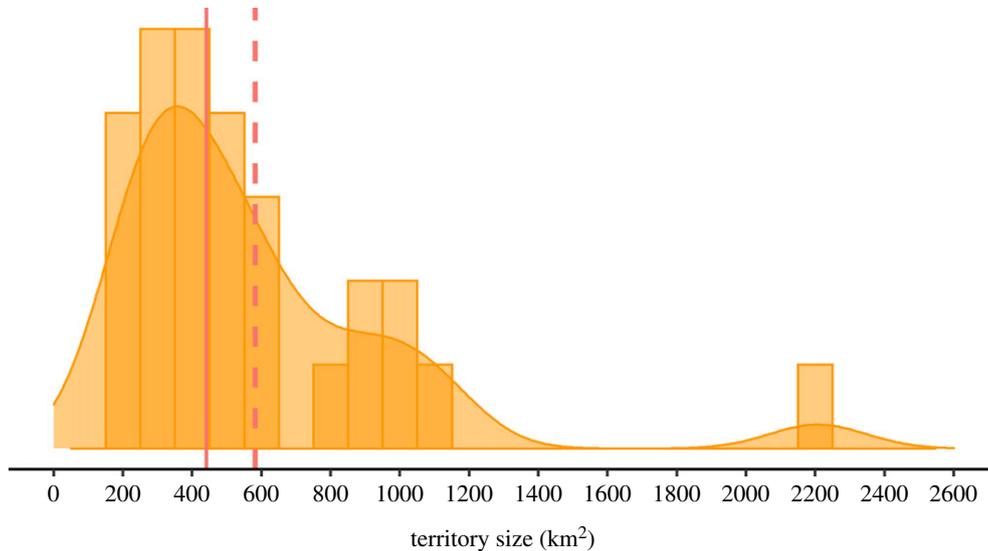
Figure 3. Histogram of 28 territory sizes of wolves, overlaid with a density plot, mean size (dashed vertical line) and median size (solid vertical line). (Online version in colour.)

deer winter density index, and for elk summer and winter density indices. The long-term regional averages were the most reliable ungulate abundance data for our study area and provided a preliminary density estimate (the first half of the formula). The second half of the formula adjusted this index slightly lower or higher based on the relative CPUE, which generally correlates with deer and elk abundance [22,45] and is best compared within administrative regions given spatially similar factors that can affect hunting success (e.g. terrain, vegetation, accessibility, etc.). We calculated a moose density index for each cell i delineated as seasonal moose habitat as

$$\text{moose density (season)}_i = N_{\text{HD}} \div \Sigma_{\text{HD area}}.$$

N_{HD} was MFWP's estimate of moose abundance in the hunting district (HD) in which i fell, and $\Sigma_{\text{HD area}}$ was the area of summer or winter moose habitat in that HD. In limited cases where density estimates were unavailable within territories partially overlapping national parks, tribal reservations or neighbouring states (figure 2), we interpolated the ungulate indices through inverse distance weighting using the gstat package in R [46]. We smoothed each index using $9 \times 9 \text{ km}^2$ weighted moving windows. We then calculated overall ungulate density by summing the ungulate indices for each season. Our 1 km^2 resolution enabled estimating the mean value of the indices within each KDE boundary.

Competitor density was based on neighbouring groups. Each year, MFWP wolf specialists monitored all known wolf groups to estimate territory centroids (figure 2). We defined neighbours as groups whose territory centroids were within 25 km of a KDE boundary [22]. For each KDE, we calculated the mean number of neighbouring groups in year T and $T + 1$. Following [22], we standardized the number of neighbours as competitor density per 100 km^2 in territory area (because larger territories tend to have more neighbours; [22]).

Group size was the mean of sizes reported in year T and $T + 1$ (figure 2). MFWP wolf specialists reported group sizes each calendar year. We included known removals (harvest, dispersal, etc.) because these individuals were present for part of the year.

We estimated terrain ruggedness with the vector ruggedness measure [47] using R package spatialEco [48] and elevation data derived through package elevatr [49]. Higher values estimated by this index represented more rugged terrain. We calculated the mean ruggedness within each KDE. We also used the most recent road dataset (geoinfo.msl.mt.gov) to calculate the mean density of low-use roads within each KDE.

We calculated the mean human density per KDE based on 2010 census data (geoinfo.msl.mt.gov). We identified the number of hunter-reported harvest locations (wolves killed via hunting and trapping) within the KDE in year T and $T + 1$.

(c) Analyses

We analysed patterns in territory size using generalized linear mixed effect models (GLMMs) in R [38] using package lme4 [50], dplyr [51] and AICcmodavg [52] and plotted results with ggplot2 [53], jtools [54] and cowplot [55]. We first created simple GLMMs for each variable as a single fixed effect plus a random effect for group identity (family = Gaussian, link = log). We included quadratic terms for ruggedness and each mortality risk variable to test for a curvilinear relationship (table 1). We considered predictions to have support if the 90% confidence intervals (CIs) of the fixed effect's coefficient estimate did not overlap 0.

To analyse which variables most parsimoniously explained patterns in territory sizes, we created complex GLMMs with multiple fixed effects plus a random effect for group identity (electronic supplementary material, appendix SA). We started with a global model containing all variables, then developed 14 reduced models containing each 1-, 2- and 3-way combination of the benefits and costs (i.e. food alone, food and competition, etc.). We identified the most supported models using Akaike's information criterion corrected for small sample size (AICc) [56] with a cut-off of ΔAICc = 2 [57]. Results were based on centred and scaled variables (units accordingly were standard deviations from the mean).

4. Results

GPS collars were deployed on 93 wolves and collected data from 1 January 2014 to 20 May 2019. Mean collar deployment length was 10.20 months, primarily because of collar failures ($n = 36$), harvest ($n = 21$) and other mortalities ($n = 22$). Of 15 identified dispersals, 9 led to joining or forming other territories, 3 yielded mortalities and 3 yielded emigrations to nearby states.

From the wolf location data, we estimated 43 territories of 28 groups (figure 2). After averaging by group, mean territory size was 582.02 km^2 for 95% KDEs, and territories were highly variable around this mean (figure 3 and table 2).

Table 2. Mean sizes of wolf territories.

measurement	n groups	$\bar{x}$ area (km^2)	s.d. (km^2)	min (km^2)	max (km^2)	median area (km^2)
95% KDEs	28	582.02	420.21	187.71	2207.42	441.37
90% KDEs	28	440.89	390.86	137.82	1592.00	341.70
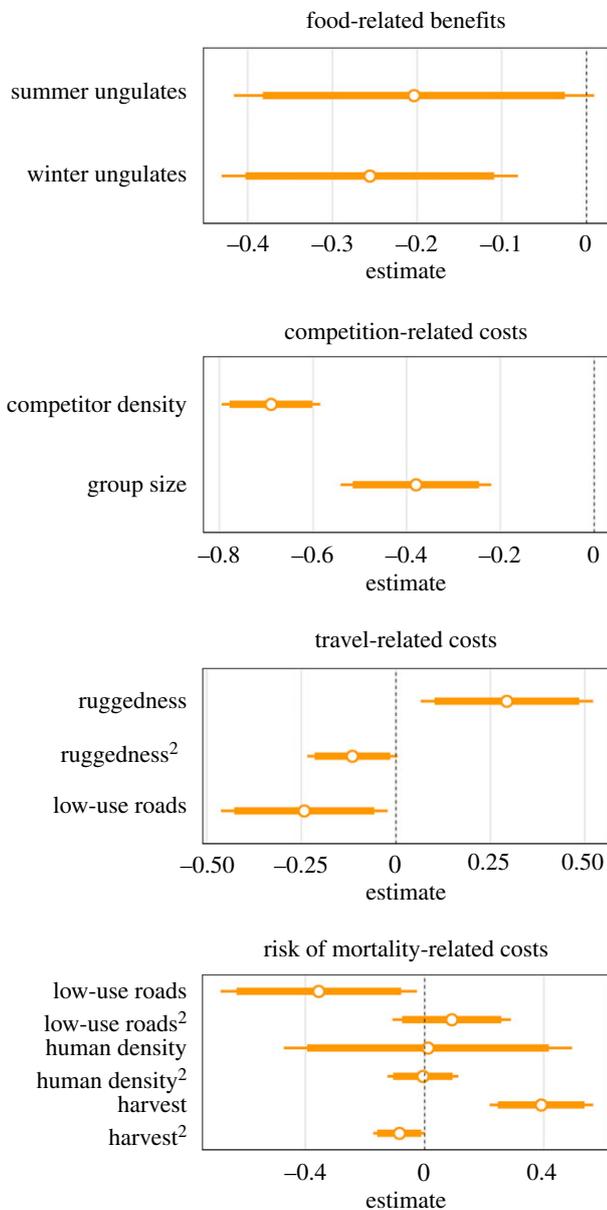
Figure 4. Patterns associated with annual space use. Lines depict 90% confidence intervals (CIs), thin tails represent 95% CIs, and points represent mean estimates. Quadratic terms tested for a curvilinear response. (Online version in colour.)

Collars averaged 1.8 fixes per day and estimates of territory size did not vary as a function of number of fixes ($p = 0.487$).

Our primary analysis revealed that territories were smaller in areas of greater ungulate densities, in areas with greater competitor densities, and for groups of greater size (figure 4). Territories had an n-curvilinear response to terrain ruggedness (i.e. increasing and then decreasing curvilinearly), with lower log likelihoods than for the linear model (electronic supplementary material, appendix SA). The greater density of low-use roads was associated with smaller territories.

There was no evidence of a curvilinear response to low-use roads or human densities. Territory size had an n-curvilinear response to harvest mortalities.

The top complex GLMM had no competing models less than 2 ΔAICc (electronic supplementary material, appendix SA). The model included variables for food, competition, and mortality risk (figure 5). Territory size had a negative relationship with the winter ungulate index, competitor density and group size, and ambiguous relationships with the summer ungulate index, human density and harvest mortalities.

5. Discussion

Territories that maximize benefits and minimize costs of ownership should lead to higher fitness [12–14]. Accordingly, as a product of natural selection [15], animals are presumably adapted to select territories economically [12]. We tested predictions from a recently developed mechanistic model for territory selection [11] to determine whether the model explained observable patterns in space use. Grey wolves served as a case study. Contrasting many mechanistic models of space use founded on a random walk framework of movement [5], this model was founded on optimal foraging theory and therefore an evolutionary approach to understanding behaviour. Integration of optimal foraging theory into mechanistic models of space use is crucial for understanding proximate and ultimate mechanisms driving spatial behaviour [5]. Importantly for conservation, inferences based on causal mechanisms are most reliable for predicting the effects of conservation actions and environmental change. Our study provides evidence for the economical selection of territories as a causal mechanism underlying ecological patterns observed in a cooperative carnivore. Empirically observed patterns in space use were consistent with hypotheses and predictions from the model. As predicted, territories were smaller in areas with greater densities of prey, competitors and low-use roads, and for groups of greater size. Territory size increased before decreasing curvilinearly with greater terrain ruggedness and harvest mortalities. Results demonstrate how a wide range of environmental and social conditions will influence economical behaviour and resulting space use.

Exclusive access to food resources is often expected to be a primary benefit of territoriality [2,12,16,17], but resulting effects on space use may be complex. Aligning with predictions of the mechanistic model [11], space use decreased with greater densities of prey (figure 4). This is consistent with other populations of wolves [58–60] and many territorial mammals ranging from other apex predators (e.g. lions, *Panthera leo* [44]) to small mammals (e.g. eastern chipmunks, *Tamias striatus* [61]). However, based on our top complex model (figure 5), territory sizes in our system may be shaped more by food resources available in winter than summer. Although more precise data for food resources could reveal the importance of summer ungulate densities, these results align with
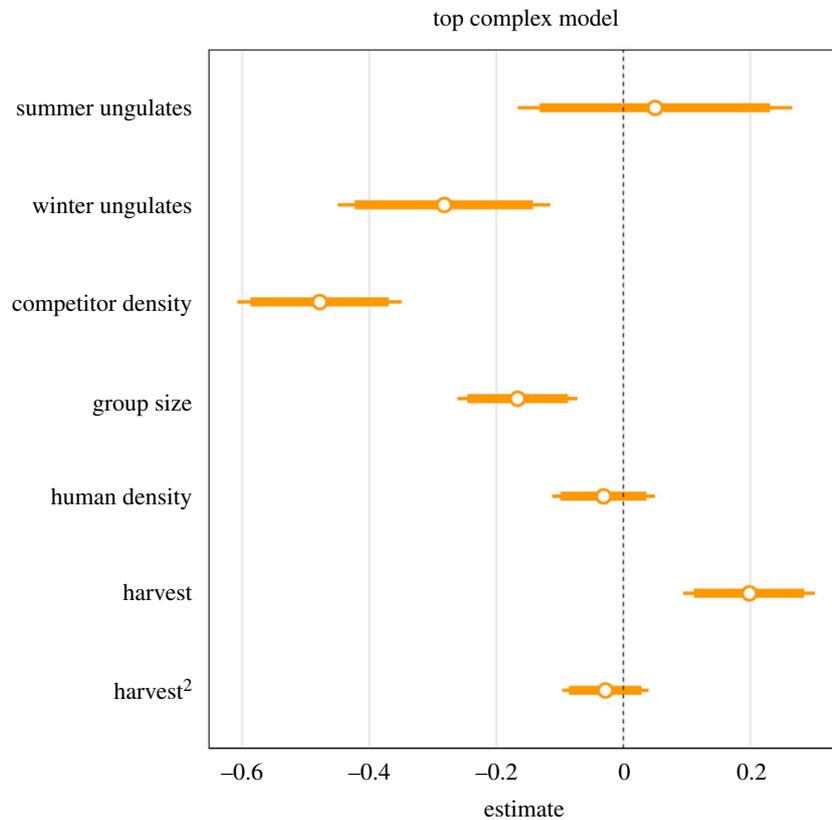
Figure 5. Variables in the top complex model for space use. Lines depict 90% CIs, thin tails represent 95% CIs, and points represent mean estimates. (Online version in colour.)

the expectation that temporal variation in food resources influences decisions about space use. This has likewise been demonstrated for lions whose space use appears to be seasonally driven by different prey species [44]. Ungulates in our system are partially migratory, and winter range can contain larger aggregations in confined areas. Dispersal of individuals in our system peaks in winter [62], meaning many territories are selected when winter prey resources are probably prioritized. Denning sites are likewise selected when many ungulates are on winter range. Wolves may therefore optimize their space use first to prey available in winter, then summer. In our system, this may contribute to an increased reliance on smaller prey in summer (e.g. beavers, *Castor canadensis* [25]). Variable effects of seasonally changing food resources should be considered when predicting how animal space use will respond to changing environmental conditions.

Competition is inherent to territoriality and should be a primary cost of space use [11,12,16,17]. Costs associated with competition reduce net gain rates of contested space, whether through exploitative or interference competition. For non-territorial individuals attempting to exploit the same food resources, larger home ranges are likely to be needed to meet resource requirements as net gains decline with increased competition [8]. By contrast, when the benefits outweigh the costs of defense, successful repulsion of competitors from a territory can protect food resources to retain greater net value and thus reduce the area required. As competitors settle nearby and compete for space, territory compression is economical as territory edges become increasingly costly to maintain [11]. As expected, territories in our system were smaller in areas of greater densities of neighbouring territories (figure 4 and table 1). Also as expected, territories were 26% smaller than observed at lower population densities [22]. In other similar

systems, territories shrank by as much as 68% as the density of territories increased [63]. Similarly among other territorial mammals, red squirrels (*Tamiasciurus hudsonicus*) [64] and European badgers (*Meles meles*) [65] expanded their territories when vacant areas appeared. Due to territory compression and expansion in response to fluctuating competition, populations with relatively stable spatial distributions cannot be assumed to have stable dynamics in competition and densities within.

Territory holders with lower competitive ability may pay higher costs to compete against more-competitive conspecifics [11]. Among social carnivores, competitive ability appears linked to group size [18–20]. As predicted if cost of competition varies inversely with group size (figures 4 and 5; table 1), territories were smaller for groups of greater size in this high-density population (estimated at 16 individuals per 1000 km^2 in occupied range [66]). This pattern may be counterintuitive at first glance if one assumes larger groups require greater area to provide sufficient food resources. However, larger territories do not necessarily provide more resources, particularly after accounting for energetic costs of maintaining a large territory. If animals defend areas to satisfy energetic requirements, territories will be smaller in areas with more food resources (table 1). Larger groups may instead kill prey at higher rates to meet fluctuating resource requirements, as observed in a nearby system [67]. This negative relationship between group size and area used has been reported for wolves elsewhere [68] and in other social mammals, including dingoes (*Canis lupus dingo* [69]). However, this pattern is expected to differ depending on whether social territorial animals are contractionists (i.e. limit group size to what can be sustained in the territory) or expansionists (i.e. expand a territory to accommodate more group members [11,44,70]). Wolves and dingoes

appear to be contractionists; in contrast, expansionism has been observed in other carnivores such as spotted hyenas (*Crocuta crocuta* [71]), lions [44,72] and Ethiopian wolves (*Canis simensis* [73,74]). The mechanistic model predicted larger territories with increasing resource requirements, but would apply explicitly to expansionists if modified to include a demographic component and a function to scale resource requirements with group size [11].

In territorial animals, competition may play particularly important roles at certain times of year. Seasonal peaks in concentrations of prey would probably attract competitors, making competitive ability especially important at these times. Additionally, if young take many months to achieve full size and the ability to travel throughout the territory, young will probably make few contributions to competition for space until they have grown. In fecund species like wolves, which produce an average of 5–6 pups each spring [32], the competitive abilities of groups have the potential to quickly change and reach full potential as young reach adult size in winter [23,32]. Dynamics in competitive pressure among neighbours in such systems are likely to be in constant flux given the fluidity in competitive ability of nearby groups. If groups need to increase their competitive ability to defend space, they may also be more willing to accept immigrants at the most competitive times of year. The decision of many individuals to disperse in winter in our system [62] could be influenced by increased acceptance of immigrants by prospective groups.

Travel is probably a primary cost of territoriality because energy is needed to access and defend resources [8–11]. Costs of travel are influenced by numerous environmental variables and a species's evolutionary traits [26,75]. We expected costs of travel to increase with terrain ruggedness and decrease with low-use roads in our system (table 1) [21,27–29]. As expected, space use increased and then decreased curvilinearly with greater terrain ruggedness (figure 4), suggesting that larger territories help offset costs of ownership until such trade-offs become uneconomical [11]. Similarly, territories were smaller in areas with more low-use roads (figure 4), suggesting that low-use roads decrease the cost of territory ownership by reducing the cost of travel. Wolves have been shown to favour human-created linear features for travel, which can decrease the energetic costs of locomotion to facilitate greater efficiency while hunting or defending space [21,27–29]. Although it might be expected that less costly travel would encourage larger territories, our results provide evidence that areas with low-use roads increase the economic value of a territory such that less space is needed to meet resource requirements. Other large carnivores also prefer roads for travel and use them to increase movement speeds and daily travel distances, including black bears [29]. Increased predator movement rates can impact prey populations, as of concern for woodland caribou (*Rangifer tarandus caribou*) in North America [28,29]. Smaller territories in areas of greater densities of low-use roads may enable predator densities to reach higher levels than would be observed without these human influences, which may further influence prey populations. These interactions between anthropogenic landscape changes, predator space use, and effects on prey will provide challenges to conservationists and land managers when evaluating the effects of building and maintaining linear features like roads.

Mortality risk may also be a primary cost of territoriality if it affects how animals select and use their territories. As predicted (table 1) [11], territory sizes in our system increased and decreased curvilinearly with increasing harvest mortalities (figure 4). Like many large carnivores, our study species often avoids humans and areas associated with human hazards [33–35]. The curvilinear response suggests that avoiding areas perceived as high mortality risk may necessitate territory expansion to offset resources lost by avoidance. Eventually, this expansion may become uneconomical, causing territories to contract as other trade-offs are made [11]. Variables related to human presence had ambiguous effects (figure 4), providing evidence that direct mortality hazards may influence the economic valuation of space use more than human presence alone in populations managed through harvest. The ability to influence spatial behaviour and resulting territory sizes and densities can be useful for conservationists aiming to manage predator or prey populations.

Like any study, ours carried various assumptions and provides avenues for future research. We selected 95% KDEs to delineate territories based on similar approaches taken for other large carnivores, and other methods (e.g. minimum convex polygons) may reveal different patterns [76]. We assumed our covariate data were of sufficient quality to detect patterns and expect some variables might demonstrate stronger or more precise relationships with territory size if more detailed data were available. There is also continued opportunity to compare and contrast the predictive strengths of this versus other mechanistic modelling approaches employed to study and explain animal space use. Finally, our present study aimed to assess evidence of economical space use in one system. We expect future research will continue to accumulate evidence of economical territory selection in other systems. The mechanistic model provides a foundation for future modifications and extensions to continue to understand animal space use [11].

6. Conclusion

We present evidence that economical space use is a causal mechanism underlying ecological patterns observed in a territorial, cooperative carnivore. Environmental and social conditions can strongly influence economical behaviour and resulting space use. Because territoriality directly affects population dynamics, changing environmental and social conditions can have profound implications for a population. This may, in turn, directly affect other populations in the ecological community. Our mechanistic approach provides a greater understanding of how and why animals decide to defend particular territories. This knowledge can be used to enhance conservation efforts and predict the effects of conservation actions. Decisions are most likely to achieve conservation objectives when founded on a strong scientific understanding of animal behaviour and the resulting effects on space use and population structure.

References

1. Burt WH. 1943 Territoriality and home range concepts as applied to mammals. *J. Mammal.* **24**, 346–352.

2. Adams ES. 2001 Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* **32**, 277–303. (doi:10.1146/annurev.ecolsys.32.081501.114034)

3. Brown JL, Orians GH. 1970 Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* **1**, 239–262.

4. Maher CR, Lott DF. 2000 A review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.* **143**, 1–29. (doi:10.1674/0003-0031(2000)143[0001:AROEDO]2.0.CO;2)

5. Börger L, Dalziel BD, Fryxell JM. 2008 Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecol. Lett.* **11**, 637–650. (doi:10.1111/j.1461-0248.2008.01182.x)

6. Potts JR, Lewis MA. 2014 How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proc. R. Soc. B* **281**, 20140231.

7. Lewis MA, Murray JD. 1993 Modelling territoriality and wolf-deer interactions. *Nature* **366**, 738–740.

8. Mitchell MS, Powell RA. 2004 A mechanistic home range model for optimal use of spatially distributed resources. *Ecol. Modell.* **177**, 209–232. (doi:10.1016/j.ecolmodel.2004.01.015)

9. Mitchell MS, Powell RA. 2007 Optimal use of resources structures home ranges and spatial distribution of black bears. *Anim. Behav.* **74**, 219–230. (doi:10.1016/j.anbehav.2006.11.017)

10. Mitchell MS, Powell RA. 2012 Foraging optimally for home ranges. *J. Mammal.* **93**, 917–928. (doi:10.1644/11-MAMM-S-157.1)

11. Sells SN, Mitchell MS. 2020 The economics of territory selection. *Ecol. Modell.* **15**, 109329.

12. Brown JL. 1964 The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**, 160–169. (doi:10.1017/CBO9781107415324.004)

13. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

14. Krebs JR, Kacelnik A. 1991 Decision-making. In *Behavioural ecology: an evolutionary approach*, 3rd edn (eds JR Krebs, NB Davies), pp. 105–136. Oxford, UK: Oxford University Press.

15. Darwin C. 1859 *On the origin of the species*. London, UK: John Murray.

16. Carpenter FL. 1987 Food abundance and territoriality: to defend or not to defend? *Am. Zool.* **27**, 387–399. (doi:10.1093/icb/27.2.387)

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

18. Cassidy KA, MacNulty DR, Stahler DR, Smith DW, Mech LD. 2015 Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behav. Ecol.* **26**, 1352–1360. (doi:10.1093/beheco/arv081)

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

20. Sillero-Zubiri C, Macdonald DW. 1998 Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *J. Zool.* **245**, 351–361. (doi:10.1017/S0952836998007134)

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

22. Rich LN, Mitchell MS, Gude JA, Sime CA. 2012 Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. *J. Mammal.* **93**, 722–731. (doi:10.1644/11-MAMM-A-079.2)

23. Mech LD, Boitani L. 2003 Wolf social ecology. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 1–34. Chicago, IL: University of Chicago Press.

24. Mech LD, Peterson RO. 2003 Wolf-prey relations. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 131–160. Chicago, IL: University of Chicago Press.

25. Peterson RO, Ciucci P. 2003 The wolf as a carnivore. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 105–130. Chicago, IL: University of Chicago Press.

26. Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013 Energy landscapes shape animal movement ecology. *Am. Nat.* **182**, 298–312. (doi:10.1086/671257)

27. Zimmermann B, Nelson L, Wabakken P, Sand H, Liberg O. 2014 Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav. Ecol.* **25**, 1353–1364. (doi:10.1093/beheco/aru134)

28. Dickie M, Serrouya R, McNay RS, Boutin S. 2017 Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* **54**, 253–263. (doi:10.1111/1365-2664.12732)

29. Dickie M, McNay SR, Sutherland GD, Cody M, Avgar T. 2020 Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *J. Anim. Ecol.* **89**, 623–634. (doi:10.1111/1365-2656.13130)

30. Fritts SH, Stephenson RO, Hayes RD, Boitani L. 2003 Wolves and humans. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 289–316. Chicago, IL: University of Chicago Press.

31. Musiani M, Paquet PC. 2004 The practices of wolf persecution, protection, and restoration in Canada and the United States. *Bioscience* **54**, 50–60.

32. Packard JM. 2003 Wolf behavior: reproductive, social, and intelligent. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 35–65. Chicago, IL: University of Chicago Press.

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

34. Latham ADM, Latham MC, Boyce MS, Boutin S. 2011 Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecol. Appl.* **21**, 2854–2865.

35. Whittington J S, Clair CC, Mercer G. 2004 Path tortuosity and the permeability of roads and trails to wolf movement. *Ecol. Soc.* **9**, 4.

36. Foresman KR. 2001 *The wild mammals of Montana*. Lawrence, KS: American Society of Mammalogists.

37. Worton BJ. 1989 Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.

38. R Core Team. 2020 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

39. Calenge C. 2006 The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519.

40. Brandell EE, Fountain-Jones NM, Gilbertson MLJ, Cross PC, Hudson PJ, Smith DW, Stahler DR, Packer C, Craft ME. 2020 Group density, disease, and season shape territory size and overlap of social carnivores. *J. Anim. Ecol.* 1–15. (doi:10.1111/1365-2656.13294)

41. Jackson CR, Groom RJ, Jordan NR, McNutt JW. 2017 The effect of relatedness and pack size on territory overlap in African wild dogs. *Mov. Ecol.* **5**, 1–10. (doi:10.1186/s40462-017-0099-8)

42. Edwards MA, Nagy JA, Derocher AE. 2009 Low site fidelity and home range drift in a wide-ranging, large Arctic omnivore. *Anim. Behav.* **77**, 23–28. (doi:10.1016/j.anbehav.2008.09.025)

43. Benson JF, Patterson BR. 2013 Inter-specific territoriality in a *Canis* hybrid zone: spatial segregation between wolves, coyotes, and hybrids. *Oecologia* **173**, 1539–1550. (doi:10.1007/s00442-013-2730-8)

44. Loveridge AJ, Valeix M, Davidson Z, Murindagomo F, Fritz H, MacDonald DW. 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. (doi:10.1111/j.1600-0587.2009.05745.x)

45. Dusek G, Wood A, Hoekman S, Sime C, Morgan J. 2006 Ecology of white-tailed deer in the Salish Mountains, Northwest Montana. Final Report, Federal Aid in Wildlife Restoration project W-120-R, Montana Fish, Wildlife, and Parks.

46. Pebesma EJ. 2004 Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* 683–691.

47. Sappington JM, Longshore KM, Thomson DB. 2007 Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* **71**, 1419–1426.

48. Evans JS. 2020 spatialEco. R package version 1.3-1. See https://github.com/jeffreyevans/spatialEco.

49. Hollister JW. 2020 elevatr: access elevation data from various APIs. R package version 0.3.1. See https://CRAN.R-project.org/package=elevatr/

50. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)

51. Wickham H, François R, Henry L, Müller K. 2020 dplyr: a grammar of data manipulation. R package version 1.0.2. See https://CRAN.R-project.org/package=dplyr.

52. Mazerolle MJ. 2020 AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. See https://cran.r-project.org/package=AICcmodavg.

53. Wickham H. 2016 Ggplot2: elegant graphics for data analysis. See https://ggplot2.tidyverse.org.

54. Long JA. 2020 jtools: analysis and presentation of social scientific data. R package version 2.1.0. See https://cran.r-project.org/package=jtools.

55. Claus OW. 2020 cowplot: streamlined plot theme and plot annotations for ggplot2. R package version 1.1.0. See https://CRAN.R-project.org/package=cowplot.

56. Burnham KP, Anderson DR. 2002 *Model selection and multi-model inference: a practical information–theoretic approach*, 2nd edn. New York, NY: Springer.

57. Anderson DR, Link WA, Johnson DH, Burnham KP. 2001 Suggestions for presenting the results of data analyses. *J. Wildl. Manage.* **65**, 373–378.

58. Fuller TK, Mech LD, Fitts-Cochran J. 2003 Wolf population dynamics. In *Wolves: behavior, ecology and conservation* (eds LD Mech, L Boitani), pp. 161–191. Chicago, IL: University of Chicago Press.

59. Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Kowalczyk R. 2007 Territory size of wolves *Canis lupus*: linking local (Białowieża Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography (Cop.)* **30**, 66–76. (doi:10.1111/j.2006.0906-7590.04826.x)

60. Kittle AM *et al.* 2015 Wolves adapt territory size, not pack size to local habitat quality. *J. Anim. Ecol.* **84**, 1177–1186. (doi:10.1111/1365-2656.12366)

61. Mares MA, Watson MD, Lacher TE. 1976 Home range perturbations in *Tamias striatus*. *Oecologia* **12**, 1–12.

62. Jimenez MD *et al.* 2017 Wolf dispersal in the Rocky Mountains, western United States: 1993–2008. *J. Wildl. Manage.* **81**, 581–592. (doi:10.1002/jwmg.21238)

63. Fritts SH, Mech LD. 1981 Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildl. Monogr.* **80**, 3–79.

64. 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. (doi:10.1139/z88-337)

65. Kruuk HH, Parish T. 1987 Changes in the size of groups and ranges of the European badger (*Meles meles* L.) in an area in Scotland. *J. Anim. Ecol.* **56**, 351–364.

66. Sells SN, Keever AC, Mitchell MS, Gude J, Podruzny K, Inman R. 2020 *Improving estimation of wolf recruitment and abundance, and development of an adaptive harvest management program for wolves in Montana*. Final Report for Federal Aid in Wildlife Restoration Grant W-161-R-1. Helena, MT: Montana Fish, Wildlife and Parks.

67. Horne JS, Hurley MA, White CG, Rachael J. 2019 Effects of wolf pack size and winter conditions on elk mortality. *J. Wildl. Manage.* **83**, 1103–1116. (doi:10.1002/jwmg.21689)

68. Mattisson J, Sand H, Wabakken P, Gervasi V, Liberg O, Linnell JDC, Rauset GR, Pedersen HC. 2013 Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia* **173**, 813–825. (doi:10.1007/s00442-013-2668-x)

69. Newsome TM, Ballard G-A, Dickman CR, Fleming PJS, 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. (doi:10.1111/j.1600-0587.2013.00056.x)

70. Macdonald DW, Johnson DDP. 2015 Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. *J. Zool.* **295**, 75–107. (doi:10.1111/jzo.12202)

71. Höner OP, Wachter B, East ML, Runyoro VA, 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. (doi:10.1111/j.0030-1299.2005.13533.x)

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

73. 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. (doi:10.1111/j.1469-7998.1995.tb02747.x)

74. Tallents LA, Randall DA, Williams SD, Macdonald DW. 2012 Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. *J. Anim. Ecol.* **81**, 24–35. (doi:10.1111/j.1365-2656.2011.01911.x)

75. Wilson RS, Husak JF, Halsey LG, Clemente CJ. 2015 Predicting the movement speeds of animals in natural environments. *Integr. Comp. Biol.* **55**, 1125–1141. (doi:10.1093/icb/icv106)

76. Fieberg J, Börger L. 2012 Could you please phrase 'home range' as a question? *J. Mammal.* **93**, 890–902. (doi:10.1644/11-MAMM-S-172.1)

77. Montana Fish Wildlife and Parks. 2005 *Biomedical protocol for free-ranging gray wolves* (Canis lupus) *in Montana: capture, anesthesia, surgery, tagging, sampling and necropsy procedures*. Bozeman, MT: MFWP Wildlife Research Laboratory.

78. Sikes RS, Gannon WL Animal Care and Use Committee of the American Society of Mammalogists. 2011 Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**, 235–253.

79. Sells SN *et al.* 2021 Data from: Evidence of economical territory selection in a cooperative carnivore. Dryad Digital Repository. (doi:10.5061/dryad.z612jm6bg)