Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana

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Territoriality in animals is of both theoretical and conservation interest. Animals are territorial when benefits of exclusive access to a limiting resource outweigh costs of maintaining and defending it. The size of territories can be considered a function of ecological factors that affect this benefit–cost ratio. Previous research has shown that territory sizes for wolves (*Canis lupus*) are largely determined by available biomass of prey, and possibly pack size and density of neighboring wolf packs, but has not been interpreted in a benefit–cost framework. Such a framework is relevant for wolves living in the Northern Rocky Mountains where conflicts with humans increase mortality, thereby potentially increasing costs of being territorial and using prey resources located near humans. We estimated territory sizes for 38 wolf packs in Montana from 2008 to 2009 using 90% adaptive kernels. We then created generalized linear models (GLMs) representing combinations of ecological factors hypothesized to affect the territory sizes of wolf packs. Our top GLM, which had good model fit ($R^2 = 0.68$, $P < 0.0005$), suggested that territory sizes of wolves in Montana were positively related to terrain ruggedness, lethal controls, and human density and negatively related to number of surrounding packs relative to the size of the territory. We found that the top GLM successfully predicted territory sizes ($R^2 = 0.53$, $P < 0.0005$) using a jackknife approach. Our study shows that territory sizes of group-living carnivores are influenced by not only intraspecific competition and availability of limiting resources, but also by anthropogenic threats to the group's survival, which could have important consequences where these territorial carnivores come into conflict with humans.

Key words: anthropogenic mortality, intraspecific competition, Montana, prey availability, territory size, wolf

Territoriality in animals is of both theoretical and conservation interest. Territories are of theoretical interest because they can vary greatly in size within species (Fuller 1989; Gompper and Gittleman 1991; Linnell et al. 2001) and causes for this variation are not always well understood (Ferguson et al. 1999; Fuller et al. 2003; Gompper and Gittleman 1991). They are of conservation interest because territoriality influences the distribution and density of animals on a landscape, in turn affecting the design of protected areas (Schwartz 1999; Woodroffe and Ginsberg 2000), monitoring methods (MacKenzie et al. 2006), and estimation of carrying capacities (Herfindal et al. 2005) or population abundances (Gros et al. 1996).

A territory is the portion of an animal's home range where intraspecific competitors are actively excluded from a particular resource or resources (Maher and Lott 1995; Powell 2000). For an animal(s) to maintain a territory, the following inequality must hold true:

$$E + T < aP + bP \qquad (1)$$

where E represents the costs of daily living, T represents the costs of monitoring, maintaining, defending, and developing the territory, P represents the limiting resource (e.g., food, nest sites, or tunnel systems), a represents the proportion of the limiting resource the animal(s) has access to if nonterritorial, and b represents the proportion of the limiting resource the animal(s) has access to if territorial (Carpenter and MacMillen 1976). The size of a territory is associated with this inequality,

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where productivity of limiting resources (P) and territory size are generally inversely related (Powell 2000). For example, when food availability is the limiting resource, food availability and territory sizes are inversely related (Carbone and Gittleman 2002; Fuller 1989; Grigione et al. 2002).

Costs associated with being territorial (T) increase with territory size, whereas benefits are asymptotic once survival and reproduction are maximized. Thus, territories commonly do not exceed the minimum size needed to supply the resources required for survival and reproduction (Powell 2000). This relationship does not necessarily hold true when a territorial animal(s) has few competitive neighbors. In this case, costs (T) are very low and territories may be larger than needed for the animal(s) to survive and reproduce (Boutin and Schweiger 1988; Krebs 1971). For territorial animals that live in groups (e.g., lions [*Panthera leo*], dingoes [*Canis lupus dingo*], or African wild dogs [*Lycaon pictus*]), the number of individuals and territory size could be positively related because larger groups require greater access to limiting resources (P) and generally have a competitive advantage in territorial competition (Grinnell et al. 1995; Mech et al. 1998). Alternatively, research has shown that territory sizes do not always increase with group size (Ballard et al. 1998; Creel and Creel 1995; MacDonald 1983), creating uncertainty about how group size contributes to variation in the territory sizes of group-living animals.

Gray wolves (*Canis lupus*) are a group-living, territorial species of conservation interest. Wolves were listed as endangered within the Northern Rocky Mountains of the United States (Northern Rockies) from 1973 until May of 2011 (United States Fish and Wildlife Service et al. 2010) and remain endangered within other portions of their global distribution. Because wolves are strongly territorial, knowing factors influencing the size of their territories in the Northern Rockies will help explain their current distribution, forecast future distributions, predict conflict with humans (Woodroffe and Ginsberg 2000), and design monitoring protocols (MacKenzie et al. 2006). Therefore, we investigated how territory sizes of wolf packs in Montana were affected by ecological factors we hypothesized may influence the benefit–cost ratio of territoriality. The limiting resource (P) for wolves is generally considered wild ungulate prey (Fuller et al. 2003; Jedrzejewski et al. 2007; Oakleaf et al 2006), such that as ungulate availability increases, territory sizes decrease (Fuller 1989; Fuller et al. 2003; Jedrzejewski et al. 2007). The ungulates actually available to wolves in the Northern Rockies may be represented by wild ungulate biomass; we hypothesized that as wild ungulate biomass increases, territory size should decrease (H_1 and H_2; Table 1). Ungulate availability may also be represented by ecological factors that indirectly influence both the distribution and vulnerability of ungulates (Garrott et al. 2009). Where wolves currently occur in the Northern Rockies, the distribution of ungulates is positively associated with forest cover (Oakleaf et al. 2006). Vulnerability of ungulates in the Northern Rockies may be negatively associated with terrain ruggedness because wolves are

TABLE 1.—Ecosystem-level variables hypothesized to influence the territory sizes of wolf packs ($n = 38$) in Montana, 2008–2009. Table includes hypothesized relationship between variables and territory size and mean ($\pm SE$), minimum, and maximum values of variables.

Variable	Hypothesized relationship	$\bar{X}$	SE	x_{min}	x_{max}
Ungulate availability					
Deer biomass[a]	H_1: −	0.03	0.002	0.01	0.05
Elk biomass[a]	H_2: −	0.01	0.001	0.002	0.02
Forest cover	H_3: −	0.69	0.031	0.19	0.90
Terrain ruggedness[b]	H_4: +	0.006	0.001	0.001	0.012
Intraspecific competition[c]	H_5: −	0.01	0.001	0.002	0.04
Pack size[d]	H_{6A}: +	7.32	0.642	1.00	21.00
	H_{6B}: −				
Human density[e]	H_7: +	5.66	1.159	0.00	30.68
Number of lethal controls[f]	H_{8A}: +	0.71	0.216	0.00	5.00
	H_{8B}: −				

[a] Buck deer or bull elk harvested per km²/hunter days for deer or elk per km².
[b] Sappington et al. 2007 index.
[c] Index of probability of intraspecific competition (# surrounding packs relative to size of territory).
[d] Minimum number of wolves documented by Montana Fish, Wildlife, and Parks in each pack.
[e] Risk of anthropogenic mortality due to proximity to humans (humans/km²).
[f] Anthropogenic mortality resulting from lethal controls (number of wolves lethally removed from pack due to livestock depredations).

coursing predators that need relatively flat terrain to run down their prey; further, rugged terrain can strongly influence the distribution of ungulates, particularly in winter (White and Garrott 2005). Wolves select forested areas (Jedrzejewski et al. 2008; Mladenoff et al. 1995; Oakleaf et al. 2006) with low levels of ruggedness (i.e., low elevations and slopes—Oakleaf et al. 2006; Paquet et al. 1996; Whittington et al. 2008). Therefore, we hypothesized that increased forest cover and decreased terrain ruggedness should result in increased ungulate availability, thus decreasing territory size (H_3 and H_4; Table 1).

Even as a primary limiting resource, prey availability is unlikely to be the only determinant of territory size for wolves. Territory sizes of wolves vary considerably in areas where ungulate availability is relatively similar (Fuller 1989; Fuller et al. 2003), suggesting that other factors, both intrinsic and extrinsic to wolf populations, could be affecting the benefit–cost relationship of territoriality. We hypothesized that intrinsic factors could include intraspecific competition and pack size. We used the number of surrounding packs relative to the size of the territory as an index of the probability of intraspecific competition. We hypothesized that territory size and intraspecific competition could be negatively related because increased competition should result in increased costs of defense (T—Mech and Boitani 2003), potentially resulting in territories being reduced to the minimum size needed for the pack to survive and reproduce (i.e., reduced T; H_5—Table 1). Pack size and territory size could be positively related if larger packs have greater food requirements and fighting abilities (Adams 2001; Messier 1985). We hypothesized that the demand for more prey (P) by larger packs could result in

larger territories where the increased costs of defense (*T*) are offset by more defenders (i.e., pack members; H_{6A}, Table 1). Alternatively, we hypothesized that pack size and territory size could be negatively related if large packs have greater hunting success (i.e., increasing *P* through greater prey mass, higher probability of multiple kills, and shorter chase distances—Creel and Creel 1995) than small packs (H_{6B}; Table 1).

An extrinsic factor that could influence the territory sizes of wolf packs is humans. Equation 1 can be modified to include the influences of humans:

$$E + T < aP + bP - cP \qquad (2)$$

where *c* represents the proportion of the limiting resource not available because of humans (R. Powell, North Carolina State University, pers. comm.). Subtraction of *cP* is justifiable because anthropogenic mortality increases with proximity to humans, causing wolves to avoid areas with high densities of humans (Fuller 1989; Murray et al. 2010). Ungulates in these avoided areas are then relatively unavailable (i.e., lowering *P*). For equation 2 to hold true, increasing values of *c* would need to be offset with increases in *P*. This requires an increase in territory size, which is ultimately limited by *T*. As a result, we hypothesized that territory size and human density could be positively related (H_7; Table 1). The influence of lethal control actions, a direct form of anthropogenic mortality, on territory sizes is unknown. Lethal control is conducted by management agencies in response to livestock depredations in the Northern Rockies (Smith et al. 2010). Pack members remaining after lethal removals are not known to avoid areas where the removals took place (M. Jimenez, United States Fish and Wildlife Service, pers. comm.). Conceivably, however, lethal controls could cause a pack to become more vigilant (i.e., increasing *E*), increase costs of territory defense (*T*) because of the reduction in defenders, or simply be associated with areas with low densities of wild ungulate prey; each of these scenarios requires relatively large territories for equation 2 to hold true. We therefore hypothesized that territory size and lethal controls could be positively related (H_{8A}; Table 1). Alternatively, if territory size is positively related to pack size (H_{6A}; Table 1), then lethal removals could result in decreased territory sizes (H_{8B}; Table 1).

Our objective was to evaluate if ungulate availability, intraspecific competition, pack size, human density, or lethal control actions affected the territory sizes of wolf packs living in Montana in 2008 and 2009. We used location data from packs that contained wolves fitted with very-high-frequency (VHF) and global positioning system (GPS) collars. We adjusted territory size estimates of packs containing only VHF-collared wolves using location data from packs simultaneously containing VHF and GPS collars, providing a large sample for testing our hypotheses.

MATERIALS AND METHODS

Study area.—Our study comprised western Montana (approximate center of study area: 46°35′N, 112°02′W) where the majority of wolves in the state are found (Sime et al. 2010). Western Montana consists of large intermountain valleys and a northern portion of the United States Rocky Mountains with 80 peaks exceeding 3,385 m (Foresman 2001). The majority of land was forest intermixed with agriculture, rangeland, and grassland (Foresman 2001). Forested areas were dominated by western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa)*, lodgepole pine (*P. contorta*), and western larch (*Larix occidentalis*—Foresman 2001). The major prey species for wolves were elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*—U.S. Fish and Wildlife Service1994), and other ungulate predators included cougars (*Puma concolor*), coyotes (*C. latrans*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and humans (Pletscher et al. 1997). Livestock production was prevalent, with cattle and sheep occurring throughout the area except for most wilderness areas and Yellowstone and Glacier national parks (United States Fish and Wildlife Service 1994). Land ownership was a mixture of public and private lands. Higher-elevation forested lands were generally public and valley bottom lands were generally private. As of 2009, the state of Montana had close to 975,000 residents (Census and Economic Information Center 2010), most of whom lived in western Montana, coincident with the distribution of wolves.

Estimating wolf pack territories.—Since 1995, personnel from the United States Fish and Wildlife Service and Montana Fish, Wildlife, and Parks (MFWP) have deployed cost-effective, VHF collars on members of as many wolf packs as possible (United States Fish and Wildlife Service et al. 2010). In 2008 and 2009, 67 wolf packs in Montana contained ≥1 VHF-collared wolf (Sime et al. 2010). Collars with GPS capabilities, however, are better suited than VHF collars for providing estimates of territories because they allow the collection of a larger number of locations around the clock and through all types of weather (Ballard et al. 1998). We therefore deployed GPS collars in wolf packs located throughout western Montana in the spring, summer, and fall of 2008 and 2009. To determine which packs were targeted for a GPS collar, we excluded packs that regularly left the study area and then selected packs that encompassed the range of the ecological factors that may influence the territory sizes of wolf packs (e.g., prey density and forest cover). We obtained estimates of territory boundaries and sizes using location data from the GPS collars. Some packs had both GPS- and VHF-collared members. For these packs, we used GPS-derived estimates to assess whether territories estimated using VHF data were comparable and thus useful for analyses despite numbers of locations per collar being below the accepted minimums for accurately estimating territories (Ballard et al. 1998; Girard et al. 2002).

Wolf specialists with MFWP live-trapped wolves using Victor foothold traps (Victor Soft Catch #3, Oneida Victor Inc., Cleveland, Ohio) modified to reduce injury. They fit 1 subadult yearling (12–22 months) or adult wolf (>22 months)

per targeted pack with a GPS7000SAW store-on-board collar that had an Argos GPS data recovery link (Lotek Engineering, Inc., Newmarket, Ontario, Canada). All GPS collars were programmed to function for 2 years and were fit with a timed release mechanism that was programmed to cause the collar to drop off after 2 years. Additionally, wolves in as many packs as possible were captured by MFWP personnel, using foothold traps and occasionally helicopter net gunning and aerial darting in the winter, and fit with VHF radio collars. All VHF collars functioned for ≥ 5 years and stayed on the wolf indefinitely. All wolves were anesthetized and handled in accordance with MFWP's biomedical protocol for free-ranging wolves (Montana Fish, Wildlife, and Parks 2005) and followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

We programmed GPS collars to collect a location (latitude, longitude) once every 3 h (i.e., 8 locations per day). GPS location data were transmitted to Argos satellites for a 6-h period once every 10 to 14 days and were retrieved using GPSPlus (Version 3.1.2, Lotek Engineering, Inc., Newmarket, Ontario, Canada). Wolves wearing VHF collars were located ≤ 2 times a month using aerial telemetry and opportunistically using ground telemetry. We imported all location data into ArcGIS 9.3.1 (Environmental Software Research Institute, Redlands, California) for analysis.

We used location data to estimate annual territories for GPS-collared wolves that had remained within an established territory for 8 to 12 months while fit with a GPS collar. To estimate territory size, we generated 90%-volume adaptive kernels (Worton 1989) in ArcGIS (Home Range Tools—Rodgers et al. 2005). We set the smoothing parameter at 80% of the reference bandwidth (h_{ref}—Kie et al. 2002) to reduce the oversmoothing that may result from the full bandwidth (Seaman and Powell 1996; Worton 1995) and to prevent the undersmoothing that may result from using least-squares cross-validation (Horne and Garton 2006; Kernohan et al. 2001). We used adaptive kernel smoothing to account for differing degrees of autocorrelation among locations (Kernohan et al. 2001; Worton 1989). We estimated 90%-volume kernels to reduce the effects of extraterritorial forays on estimates.

For wolf packs that had both GPS- and VHF-collared wolves, we also estimated 90% kernels for 2008 and 2009, separately, using VHF locations based on the same kernel parameterizations. If a pack had ≥ 1 VHF-collared wolf in both 2008 and 2009, we quantified the pack's fidelity to territory boundaries between years by overlaying annual territory estimates in ArcGIS and calculating the percent overlap (Kernohan et al. 2001). If the pack had $\geq 75\%$ territory fidelity between 2008 and 2009 we estimated its territory size using data from both years, which provided us with a larger sample size of VHF locations. If the pack had $<75\%$ territory fidelity between years we estimated its home range using data from the year with the greater number of VHF locations. We tested for a difference between territory sizes estimated using GPS and VHF location data by regressing GPS-derived territories against VHF-derived territories for those packs that carried both types of collars. If the slope estimate had a 95% confidence interval (CI) that did not overlap 1.0, we determined that VHF-derived territory estimates were likely biased and only used GPS-derived territory estimates in our analyses. If the slope estimate had a 95% CI that did overlap 1.0, we determined that GPS- and VHF-derived territory estimates were generally similar, supporting the use of territory estimates from VHF-collared wolf packs in our analyses of territory size. In this case, we constructed kernel home ranges for all remaining VHF-collared wolf packs with ≥ 10 locations during 2008–2009. Using data from both GPS- and VHF-collared wolves, we tested whether numbers of locations predicted estimates of territory size by regressing numbers of locations against territory size estimates. If the slope estimate had a 95% CI overlapping 0.0, we determined that VHF territory estimates were unlikely biased and used them in our analyses.

Ecological covariates of territory size.—We assessed a suite of ecological factors that we hypothesized could influence the territory sizes of wolf packs (Table 1). Estimates of abundance for deer and elk were not uniformly available across Montana. We therefore used hunter success in harvesting buck deer and bull elk (# harvested buck deer/hunter days for deer; # harvested bull elk/hunter days for elk) as indices of deer and elk abundance (i.e., Hamlin and Ross 2002). The harvest of antlered deer and elk is often positively correlated with the abundance of deer and elk (Dusek et al. 2006; Wood et al. 1989). We calculated deer and elk abundance for each hunting district using ungulate harvest statistics from MFWP (Montana Fish, Wildlife, and Parks 2010). In reservations and national parks where hunting was not permitted, or MFWP did not have harvest information, we estimated deer and elk abundance as the average of surrounding hunting districts for which data were available.

We also based ungulate availability on forest cover and terrain ruggedness. We estimated percent forest cover in each territory by reclassifying 90-m^2 land cover pixels (Gap Analysis Project, Wildlife Spatial Analysis Lab, University of Montana) into forest and nonforest. We used the vector terrain ruggedness index developed by Sappington et al. (2007) to assess terrain ruggedness. Ruggedness represented the average elevation change between any cell on a 200-m^2-resolution digital elevation model (United States Geological Survey National Elevation Data Set) and its adjacent cells.

We used data from MFWP's annual reports (Sime et al. 2009, 2010) to estimate intraspecific competition and pack size. We estimated intraspecific competition by calculating the number of packs known to be within 25 km (the mean diameter of an average-sized, circular territory in Montana—Sime et al. 2010) of each collared pack's territory boundary. We scaled this number to the size of the collared pack's territory because the larger the territory, the greater the area that could potentially come into contact with surrounding packs. Estimates of the number of packs and pack size were minimum estimates made by MFWP on 31 December of every
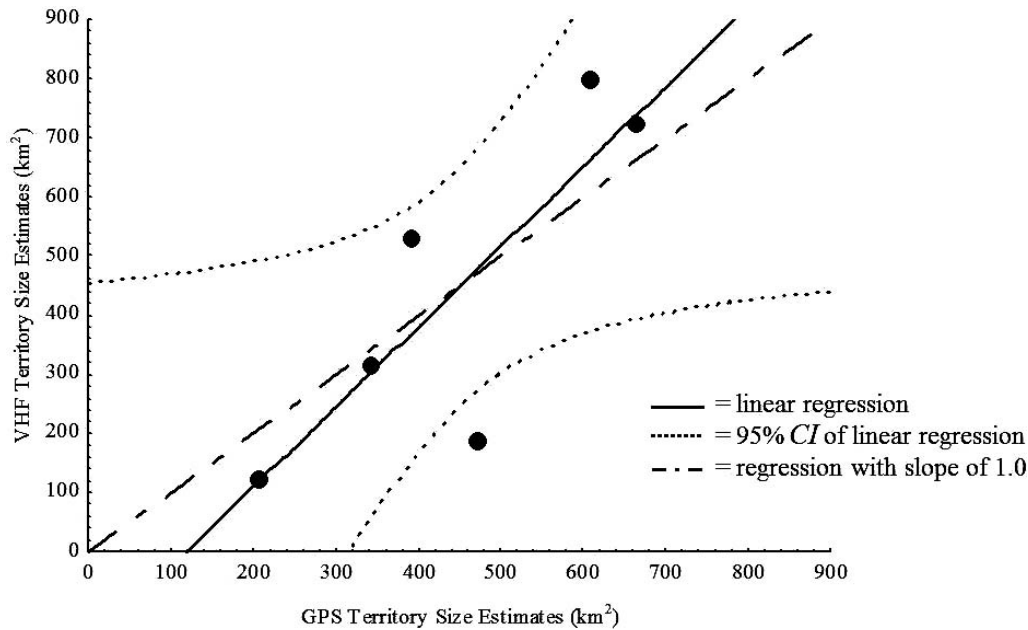
Fig. 1.—Linear regression of territory sizes estimated on the basis of global positioning system telemetry against territory sizes on the basis of very-high-frequency telemetry for 6 wolf packs in Montana, 2008–2009 with the associated 95% confidence intervals. Territories were estimated using 90% adaptive kernels.

year on the basis of aerial surveys of radiocollared wolf packs, howl, track, and scat surveys, and field verifications of reports from the general public, private landowners, and other natural resource agency personnel (Sime et al. 2010).

We also determined the mean number of wolves killed in each pack in 2008 and 2009 due to livestock depredations (i.e., lethal controls—Sime et al. 2009, 2010). We obtained data on human population density (humans/km^2) from the United States Census Bureau at the 1-km^2 cell size for the state of Montana.

Analyses.—We used generalized linear models (GLMs— McCullough and Nelder 1989) to determine covariates (Table 1) that best explained variation in the territory sizes of wolf packs in Montana. We used Spearman's rank correlation (r_s) to test for correlations among the explanatory variables; if variables were correlated ($r_s > 0.50$) we kept the variable with the greatest univariate effect size (β/SE—Zar 1999). We used a stepwise approach to develop a set of candidate models comprising different combinations of variables hypothesized to affect the territory sizes of wolf packs and used maximum-likelihood estimation (STATA 8.0; StataCorp 2007) to estimate a GLM for each model. We selected the top model set using Akaike's information criterion (AIC—Burnham and Anderson 2002) with a cutoff of $\Delta AIC = 4$ (Anderson et al. 2001). We dropped models from the top model set that included covariates with 95% CIs overlapping 0 because they contributed minimally to model fit (Arnold 2010). If >1 model remained in the top model set, we averaged parameter estimates across top models to generate the best estimated model (Burnham and Anderson 2002). We also calculated relative importance of variables by summing Akaike weights (ω_i) of models that contained each variable (Burnham and Anderson 2002).

Model evaluation.—We used a jackknife procedure (Guisan and Zimmermann 2000; Manel et al. 1999) to evaluate the predictive power of the top GLM. We estimated multiple GLMs, each time excluding a single territory size estimate. We used the fitted model for each GLM to predict the territory size excluded from the analysis. We then estimated a linear regression of observed (i.e., kernel-estimated) territory sizes against predicted territory sizes and used the slope estimate to evaluate the predictive power of the top GLM. If the slope estimate had a 95% CI overlapping 1.0 we determined that the top GLM was able to predict territory size reliably.

RESULTS

Estimating wolf pack territories.—Nine wolves and 5 wolves were fit with GPS collars in 2008 and 2009, respectively. Six of the collared wolves dispersed from the packs in which they were collared, 7 died of human-related causes (e.g., shot illegally, shot legally, or hit by car), and 6 collars stopped transmitting GPS locations after <1 year. Nonetheless, GPS-collared wolves from 9 packs provided 8– 12 months of GPS location data from within an established territory. The number of annual locations for these 9 packs ranged from 793 to 2,872 with a mean of 1,737 (*SE* = 234.7), and territory sizes ranged from 206.1 to 1,651.9 km^2 with a mean of 556.4 km^2 (*SE* = 145.43).

Thirty-six wolf packs contained ≥1 VHF-collared wolf that was located ≥10 times during 2008–2009. Six of these wolf packs had both VHF- and GPS-collared wolves. All packs had ≥75% overlap between their 2008 and 2009 territories; therefore, we combined 2008 and 2009 locations for estimating territory size. The number of VHF locations for

TABLE 2.—Top generalized linear model set for examining the spatial variation in territory sizes of wolf packs ($n = 38$) in Montana, 2008–2009. Table includes model structure, 95% confidence intervals for parameter estimates, and corresponding maximized log-likelihood (log[l]), degrees of freedom (*d.f.*), differences in Akaike's information criterion (ΔAIC), and model weights (ω; relative likelihood of models in set).

Model structure and 95% *CI*s for parameter[a] estimates	Log(l)	*d.f.*	ΔAIC	ω
$\beta_0 + R(67.34, 635.03) - C(-41.78, -23.61) + L(83.43, 201.44) + H(2.56, 22.88)$	−256.44	5	0.00	0.30
$\beta_0 + R(-7.86, 595.40) - C(-42.44, -24.18) - S(-31.41, 9.07) + L(63.96, 192.46) + H(2.07, 22.41)$	−255.76	6	0.64	0.22
$\beta_0 + R(65.62, 662.43) - C(-42.86, -22.65) + L(78.04, 201.73) + H(2.40, 23.00) - F(-5.16, 3.71)$	−256.38	6	1.88	0.12
$\beta_0 + R(62.41, 639.63) - C(-43.01, -22.28) + L(82.19, 202.55) + H(1.28, 24.05) + D(-8.67, 8.87)$	−256.44	6	2.00	0.11
$\beta_0 + R(-4.60, 621.91) - C(-42.36, 23.13) - S(-32.19, 9.01) + L(56.69, 191.86) + H(1.89, 22.50) - F(-5.40, 3.48)$	−255.65	7	2.42	0.09
$\beta_0 + R(-12.82, 599.88) - C(-44.23, -23.19) - S(-32.29, 9.40) + L(63.05, 193.58) + H(1.26, 23.97) - D(-9.58, 8.17)$	−255.74	7	2.61	0.08
$\beta_0 - C(-42.12, -23.25) - S(-37.72, 1.67) + L(39.46, 155.95) + H(1.19, 22.25)$	−257.81	5	2.73	0.08

[a] R = terrain ruggedness index (Sappington et al. 2007; change in size with every increase of 1 unit of R); C = index of the probability of intraspecific competition (change in size with each additional surrounding pack per 1,000 km^2 in territory size); L = lethal controls (change in size with each additional wolf lethally removed due to livestock depredation); H = human density (change in size with each additional person/km^2); S = pack size (change in territory size with each additional documented wolf per pack); F = forest cover (change in size with each additional % of forest cover); D = deer biomass (change in size with each additional buck deer harvested per hunter days for deer).

these 6 packs ranged from 10 to 27 with a mean of 18 (*SE* = 3.0), and territory size ranged from 122.5 to 797.4 km^2 with a mean of 445.3 km^2 (*SE* = 97.15). Despite much smaller numbers of locations using VHF telemetry, territory sizes estimated using VHF and GPS locations were generally similar ($\beta_1 = 1.35$, *SE* = 0.47, 95% *CI* = 0.43–2.27; Fig. 1). As a result, we estimated territory sizes for the remaining 30 VHF-collared wolf packs. For these packs, number of VHF locations ranged from 10 to 28 with a mean of 17 (*SE* = 1.0), and territory sizes ranged from 193.6 to 1,771.2 km^2 with a mean of 583.4 km^2 (*SE* = 56.41). Territory size estimates using GPS locations and using VHF locations were normally distributed. Mean territory size was 599.8 km^2 ($n = 38$; *SE* = 59.73), and numbers of locations did not predict estimates of territory size ($F_{1,36} = 0.19$, $R^2 = 0.01$, $P = 0.67$), indicating that VHF territory estimates were not biased ($\beta_1 = -0.03$, *SE* = 0.08, 95% *CI* = −0.19–0.13).

Analyses.—Bull elk harvest success and forest cover were correlated ($r_s = 0.65$, $P < 0.05$, $n = 38$); we kept forest cover for subsequent analyses because it had a larger univariate effect size. The top GLM ($\omega_i = 0.30$), which included terrain ruggedness, intraspecific competition, number of lethal controls, and human density, was only 1.4 times more supported than the second ranked model, which also included pack size (Table 2). The top GLM, however, was the only model within the set with ΔAIC ≤ 4 that did not include any covariates with 95% *CI*s overlapping 0.0 (Table 2); thus, we used this model as our top model and did not model average. The top GLM had good model fit ($F_{4,33} = 17.11$, $R^2 = 0.68$) and showed that territory size increased by 351.2 km^2 (*SE* = 14.48) with every increase of 1 unit of terrain ruggedness, increased by 142.4 km^2 (*SE* = 30.10) with every lethal control, increased by 12.7 km^2 (*SE* = 5.18) with every additional person/km^2, and decreased by 32.7 km^2 (*SE* = 4.63) with every surrounding pack per 1,000 km^2 in territory size (Table 2). Human density, lethal controls, and intraspecific competition were the most important covariates for explaining variation in the territory sizes of wolf packs ($\Sigma\omega_i = 1.0$), followed closely by terrain ruggedness ($\Sigma\omega_i = 0.92$), and then pack size ($\Sigma\omega_i = 0.47$), forest cover ($\Sigma\omega_i = 0.21$), and deer abundance ($\Sigma\omega_i = 0.19$). For all models within the top model set, the effects of intraspecific competition, forest cover, and pack size were negative and the effects of terrain ruggedness, lethal controls, and human density were positive (Table 2). The directionality of these parameters was consistent with our hypotheses and provided support for 1 of our 2 competing hypotheses for both pack size and lethal controls (Table 1). The effect of deer abundance, however, was not consistent with our hypothesis (Table 1) because it changed between positive and negative within the top model set (Table 2). Forest cover, pack size, and deer abundance all had weak effects on territory size because the 95% *CI*s for their respective coefficients consistently overlapped 0.0 (Table 2).

Model evaluation.—The linear regression of observed territory sizes on predicted territory sizes had a slope estimate with a 95% *CI* overlapping 1.0 ($\beta_1 = 0.88$, *SE* = 0.14, 95% *CI* = 0.60–1.16), indicating that the top GLM was able to predict territory size accurately, and predictions of territory size were consistently reliable ($F_{1,36} = 40.05$, $R^2 = 0.53$, $P < 0.0005$; Fig. 2).

DISCUSSION

We evaluated ecological factors that could potentially explain variation in the territory sizes of 38 wolf packs located throughout western Montana. We found that territory sizes of wolves were associated with not only intraspecific competition (i.e., density of packs) and availability of limiting resources (e.g., wild ungulates), but also with extrinsic factors such as threats to pack member's survival (e.g., anthropogenic mortality). As we hypothesized, territory sizes were positively related to terrain ruggedness. We assumed that terrain ruggedness represented the energetic costs a pack had to expend to find, run down, and successfully kill prey. If our assumption was valid, then our results suggest that as terrain ruggedness (i.e., cost) increased, prey vulnerability and thus biomass of prey available to wolves (P) decreased. This decrease in available prey biomass, the limiting resource for wolf populations (Fuller et al. 2003; Messier 1985; Oakleaf et al. 2006), resulted in larger territories that likely supplied more prey to offset costs of obtaining prey in rugged terrain. The observed negative relationship between forest cover and
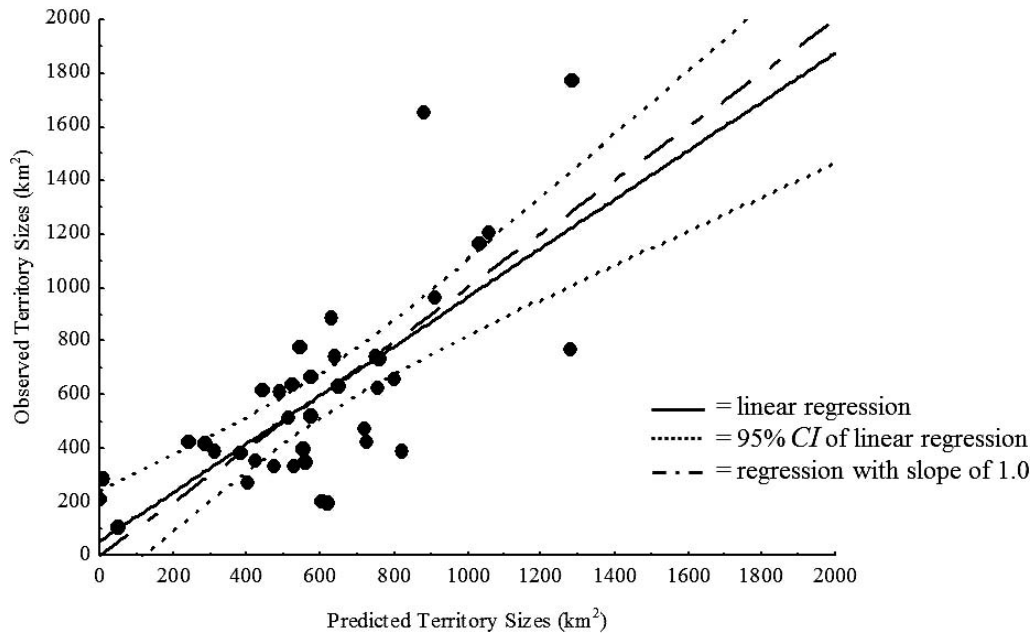
FIG. 2.—Linear regression of observed territory sizes on predicted territory sizes for 38 wolf packs in Montana, 2008–2009 with the associated 95% confidence intervals. Observed territory sizes were estimated using 90% adaptive kernels. Predicted territory sizes were estimated using a generalized linear model ($y = \beta_0 + \beta_1$[terrain ruggedness] $+ \beta_2$[number of surrounding packs relative to size of territory] $+ \beta_3$[# of lethal controls] $+ \beta_4$[human density]) and jackknife procedure (Manel et al. 1999).

territory size was also consistent with our hypothesis. This suggests that as forest cover increased, the biomass of ungulates available to wolves (P) increased, resulting in smaller territories due to the high availability of prey. Evidence to support the negative relationship between forest cover and territory size, however, was relatively uncertain (95% *CI* for coefficient included 0; Table 2); the weak relationship may have been because the majority of wolves are currently located in the western part of the state, which is heavily forested. If our hypothesis is correct, when wolves begin to establish packs in eastern Montana, where forest cover is limited, forest cover could become a more important determinant of territory sizes. We predict that territory sizes in eastern Montana should be larger than those in western Montana.

We found that deer biomass, represented by hunter success in harvesting buck deer, had an ambiguous and weak relationship with the territory sizes of wolf packs (estimates of β were both positive and negative, 95% *CI*s for coefficients included 0; Table 2). We assumed buck deer harvest represented deer biomass. If this assumption was valid, then our results suggest that absolute deer biomass was not as important as the biomass of deer actually available to wolves, as we modeled it using terrain ruggedness. If deer biomass was high and relatively uniformly distributed across western Montana, then variation in the vulnerability of deer to predation across the landscape should have a stronger relationship to territory size than biomass. In the future, however, if deer biomass declines with increasing wolf densities, it could become a more important determinant of territory size as has been found in other studies (Fuller et al.

2003; Jedrzejewski et al. 2007). Alternatively, if our assumption was not valid, then it is possible that harvest success by humans was a function of human access to places occupied by ungulates (e.g., proximity to high human densities, distance to roads, etc.), weather, or harvest regulations instead of deer densities. We did not analyze the effects of elk density on territory size because bull elk harvest success and forest cover were correlated ($r = 0.65$). This correlation provides some support for our assumption that there was a positive relationship between forest cover and the biomass of elk available to wolves (Oakleaf et al. 2006); this correlation, however, may simply reflect that hunters are more abundant in forested areas in western Montana.

As we hypothesized, territory sizes were negatively related to intraspecific competition, as represented by the number of surrounding wolf packs relative to the size of the territory. We assumed that intraspecific competition affected the amount of energy a pack had to expend directly or indirectly defending their territory from neighboring packs (T—Mech and Boitani 2003). If this assumption was valid, then our results suggest that as intraspecific competition increased, the costs of territoriality also increased. Territory sizes were negatively related to pack size but evidence to support this relationship was weak (95% *CI* for coefficient included 0; Table 2). This weak effect provides minimal support for a relationship between group size and territory size (Fuller 1989; Mech et al. 1998), adding little to the debate of whether territory size is positively (Grinnell et al. 1995) or negatively (Creel and Creel 1995) influenced by group size.

Our study was the 1st to demonstrate strong, positive associations between human density and lethal controls and

the territory size of a large carnivore. Wolves tend to avoid areas with high human densities due to increased risk of anthropogenic mortality (Murray et al. 2010); thus, we assumed that ungulates in these areas were relatively unavailable. For equation 2 to hold true, territories with relatively high human densities would need to be larger in size to compensate for the loss in ungulate availability. The impacts of lethal controls on wolf packs are less understood and, contrary to human density, lethal controls do not result in avoidance of certain areas by the remaining pack members (M. Jimenez, United States Fish and Wildlife Service, pers. comm.). We hypothesized that lethal controls could cause a pack to become more vigilant (i.e., increasing E), increase costs of territory defense (T) because of the reduction in defenders, or simply be associated with areas with low densities of wild ungulate prey (i.e., relatively small P), in each case resulting in relatively large territories. Alternatively, we hypothesized that if territory size is positively related to pack size, lethal removals could result in relatively small territories. Our analysis showed a strong, positive relationship between lethal controls and territory size; we therefore reject hypothesis H_{8B}. Although we have posited some explanations for why territory size and lethal removals could be positively related, the mechanism behind this relationship remains unclear. On one hand, the relationship may be correlative, wherein lethal controls occur in places of low wild ungulate densities; thus, prey density, not lethal controls, could be driving territory sizes. Our tests of collinearity among our explanatory variables did not, however, detect the negative correlation between prey density and lethal removals that would be expected if this relationship were true. Alternatively, lethal removals could affect wolves directly, by either the means we hypothesized (i.e., increasing E or T), or through other means, perhaps outside the benefit–cost framework we used, that we did not consider (e.g., changing the social dynamics within packs through the removal of breeders or other experienced pack members). Further exploration of the positive relationship we found between lethal controls and territory size is needed.

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