

# Interannual variability: a crucial component of space use at the territory level

ALESSIA UBONI,<sup>1,3</sup> JOHN A. VUCETICH,<sup>1</sup> DANIEL R. STAHLER,<sup>2</sup> AND DOUGLAS W. SMITH<sup>2</sup>

<sup>1</sup>*School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan 49931 USA*

<sup>2</sup>*Yellowstone Center for Resources, Wolf Project, P.O. Box 168, Yellowstone National Park, Wyoming 82190 USA*

**Abstract.** Interannual variability in space use and how that variation is influenced by density-dependent and density-independent factors are important processes in population ecology. Nevertheless, interannual variability has been neglected by the majority of space use studies. We assessed that variation for wolves living in 15 different packs within Yellowstone National Park during a 13-year period (1996–2008). We estimated utilization distributions to quantify the intensity of space use within each pack’s territory each year in summer and winter. Then, we used the volume of intersection index (VI) to quantify the extent to which space use varied from year to year. This index accounts for both the area of overlap and differences in the intensity of use throughout a territory and ranges between 0 and 1. The mean VI index was 0.49, and varied considerably, with ~20% of observations ( $n = 230$ ) being  $<0.3$  or  $>0.7$ . In summer, 42% of the variation was attributable to differences between packs. These differences can be attributable to learned behaviors and had never been thought to have such an influence on space use. In winter, 34% of the variation in overlap between years was attributable to interannual differences in precipitation and pack size. This result reveals the strong influence of climate on predator space use and underlies the importance of understanding how climatic factors are going to affect predator populations in the occurrence of climate change. We did not find any significant association between overlap and variables representing density-dependent processes (elk and wolf densities) or intraspecific competition (ratio of wolves to elk). This last result poses a challenge to the classic view of predator–prey systems. On a small spatial scale, predator space use may be driven by factors other than prey distribution.

**Key words:** *Canis lupus*; climate change; density-dependent space use; interannual variability; predator–prey relationship; space use; utilization distribution; volume of intersection; wolf packs; Yellowstone National Park, USA.

## INTRODUCTION

Extensive theory explains how space use represents an important perspective from which to understand population dynamics, including regulation, interspecific competition, and consumer–resource relationships (e.g., Morris 2003, Jonzén et al. 2004, Abrams 2007). Nevertheless, empirical assessments of such ideas are limited. One reason for this gap between theory and empiricism involves a basic difference in the way that population dynamics and space use are typically assessed. The empirical assessment of population dynamics relies greatly on quantifying interannual variation in population processes and assessing the causes and consequences of that variation.

By contrast, interannual variability is rarely the focus of inquiry in assessments of space use. We conducted a literature search on six top-ranked ecology journals

(*Ecology*, *Journal of Animal Ecology*, *Oikos*, *Journal of Wildlife Management*, *Journal of Applied Ecology*, and *Ecological Applications*), using the keywords “space use” and limiting the search to the time period 2003–2013. Methodological papers not including any case study of space use were excluded from analysis. We found that only 18% of the studies (i.e., 17 out of 94) assessed interannual variability in space use. Space use is known to depend on a number of factors that vary from year to year, such as the presence of competitors and predators (Mao et al. 2005, Benson et al. 2010, Blackie et al. 2011), climatic factors (Cotner and Schooley 2011), and differences in habitat preference among individuals (Beyer et al. 2010, McLoughlin et al. 2010). Thus, there are compelling reasons to expect space use to vary considerably and systematically from one year to the next.

A prerequisite for understanding the connection between space use and population dynamics will require a much better empirical understanding of interannual variation in space use. Here, we contribute to that prerequisite by using location data gathered throughout a 13-year period (1996–2008) from 15 wolf (*Canis lupus*)

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<sup>3</sup> Present address: Department of Ecology and Environmental Science, Umeå University, 90187, Umeå, Sweden. E-mail: auboni@mtu.edu

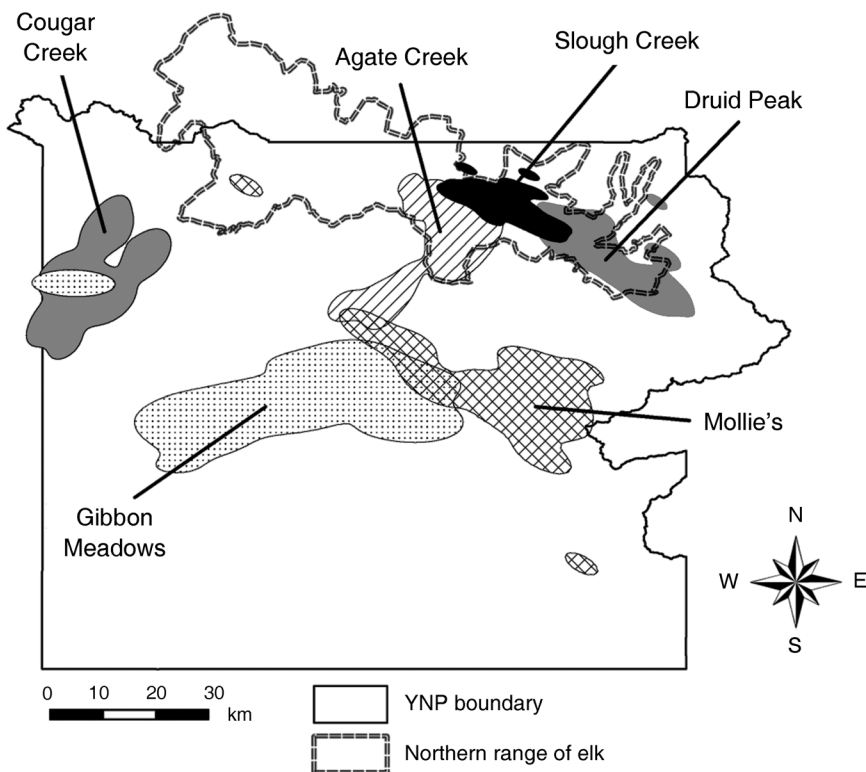


FIG. 1. Location of territorial boundaries for six wolf packs (*Canis lupus*) living in Yellowstone National Park (YNP) in summer 2008. Agate Creek (territory size 324.66 km<sup>2</sup>), Druid Peak (255.14 km<sup>2</sup>), and Slough Creek (143.88 km<sup>2</sup>) packs belonged to the Northern Range population, which preys primarily on elk from the Northern Range herd. The dashed line shows the boundaries of that elk herd. Cougar Creek (301.63 km<sup>2</sup>), Gibbon Meadows (841.21 km<sup>2</sup>), and Mollie's (566.04 km<sup>2</sup>) packs belonged to the Interior population. This map is generally representative of pack locations throughout the study period, 1996–2008.

packs living in Yellowstone National Park to assess interannual variation in space use at the territory level (Johnson 1980). Wolves are generalist predators (Mech and Boitani 2003), and their plasticity in the use of resources (e.g., prey and habitat; Gervasi et al. 2013) makes them perfect candidates for analyzing temporal variability in space use. Our basic approach begins by quantifying the extent to which utilization distributions (Seaman and Powell 1996) for a particular pack overlap between years. Then, we use regression analysis to assess the extent to which that overlap was associated with various temporally dynamic aspects of the environment, such as density-independent (e.g., climate) and density-dependent environmental factors (e.g., prey density). Prey and competitor densities are expected to be of particular importance in shaping the spatial dynamics of a top-order predator.

## MATERIALS AND METHODS

### *Study system*

Yellowstone National Park (YNP) is located in the central Rocky Mountains, USA, and has an area of 8990 km<sup>2</sup>. The park is inhabited by a well-studied population of wolves (e.g., Smith et al. 2004, Coulson et al. 2011, Metz et al. 2012) that is frequently represented as two

subpopulations, one living on the Northern Range (1526 km<sup>2</sup>) and the other in the interior portion of the park (7900 km<sup>2</sup>) (Fig. 1). Elk (*Cervus elaphus*) are the dominant prey of Northern Range wolves, whereas bison (*Bison bison*) represent a larger share of diet for Interior wolves (Smith et al. 2004). During the study period (1996–2008), wolf density on the Northern Range varied from 13 to 64 wolves/1000 km<sup>2</sup> and from 2 to 9 wolves/1000 km<sup>2</sup> in the interior portion of the park. Average pack size was 13.5 wolves and average territory size was 282.82 km<sup>2</sup> on the Northern Range, whereas in the interior, average pack size was 12.0 wolves and average territory size was 873.68 km<sup>2</sup> (summer estimates). The wolf population in the park was formed from a reintroduction program started in 1995.

Elevation in the park ranges between 1500 and 3500 m. The dominant vegetative communities are steppe, shrub-steppe, conifer forests, and aspen stands (Despain 1990). Winters are usually cold and snowy, and summers are dry. At lower elevations (northern portion of YNP), average annual precipitation is ~25 cm, of which 30–35% is snow. Annual precipitation at higher elevations averages 180 cm, primarily in form of snow (Farnes et al. 1999).

### Field methods and location data

Between 1996 and 2008, we radio-collared wolves from each pack in YNP. Some wolves ( $n = 289$ ) were outfitted with VHF radio collars (Telonics, Mesa, Arizona, USA). A different set of wolves ( $n = 34$ ) were outfitted with downloadable GPS collars: Televilt (Lindesberg, Sweden), Telonics (Mesa, Arizona, USA), and Lotek (Newmarket, Ontario, Canada). These collars recorded locations every 30 minutes throughout the summer and every 3 hours throughout the winter. Locations from VHF collars were recorded approximately once a week from January to September, except during the month of March, when locations were gathered as frequently as once a day. For additional details on the methods used to capture, handle, and locate wolves, see Metz et al. (2012).

We combined these two radiotelemetry data sets to estimate seasonal utilization distributions, UD<sub>s</sub> (Seaman and Powell 1996) for each wolf pack. To make the two data sets comparable, we used GPS locations gathered only during daylight hours. To avoid autocorrelation among locations separated by short periods of time (Otis and White 1999), we randomly culled observations so that the data sets included only a single location per pack per day throughout the winter (January–March). During the summer (April–September), packs are less cohesive and each pack is routinely characterized by small, semi-independent groups of wolves (Metz et al. 2012). Therefore, we constructed UD<sub>s</sub> for summer using one randomly selected location per group per day. To perform this random culling, we used the extension Hawth's Analysis Tools for ArcGIS (Beyer 2004). The wolves in our sample lived in 15 different packs (Appendix A: Table A1).

### Assessing interannual variability

We quantified interannual variability in space use among packs during each of two seasons, summer (April–September) and winter (January–March), defined according to wolf biology in the study area (Smith et al. 2009). Our first step was to calculate UD<sub>s</sub> for each wolf pack for each of these two seasons. A UD is a probability density function ( $\hat{f}_{UD}(x,y)$  at location  $[x, y]$ ) that estimates the intensity of use for every point of a home range. We calculated UD<sub>s</sub> using the fixed-kernel technique (Seaman and Powell 1996, Kernohan et al. 2001) with the “plug-in” method for bandwidth selection (Wand and Jones 1995, Gitzen et al. 2006), which is available in the “ks” library for R version 2.15.0 (R Development Core Team 2013). We eliminated the outer 5% of the UD<sub>s</sub>, based on volume, to lower the risk of spurious results created by including low-use areas on the tails of the probability density function (Vanak and Gompfer 2010). Because the fixed-kernel technique only gives reliable results if at least 30 locations are used (Seaman et al. 1999), we limited our analysis to packs with more than 30 locations for any given season.

Fifteen packs met this requirement (Appendix A: Table A1).

The second step of our analysis was to quantify the overlap in space use between years for a particular pack inside its territory during a particular season (summer or winter). To do this, we calculated the volume of intersection (VI) index between two years,  $i$  and  $j$ :

$$VI_{i,j} = \iint \hat{f}_i(x,y), \hat{f}_j(x,y) dx dy$$

where  $\hat{f}_i$  and  $\hat{f}_j$  are the UD<sub>s</sub> for years  $i$  and  $j$ , respectively, for a particular season (Seidel 1992, Millsbaugh et al. 2004). The VI index measures overlap between the two UD<sub>s</sub> in a three-dimensional way, accounting not only for the perimetral overlap (two-dimensional overlap), but also for how the shapes of the two UD<sub>s</sub> overlap. In other words, VI can be used to quantify the intensity of overlap in space use. The VI index ranges from 0, representing no overlap, to 1, representing total overlap (Seidel 1992, Millsbaugh et al. 2004). The VI index has been used, for example, to assess seasonal variation in space use of Indian foxes and spotted skunks (Lesmeister et al. 2009, Vanak and Gompfer 2010). Here, we use VI to represent interannual variation in space use.

The VI index varied considerably among packs and pairs of years (see *Results*). To better understand the causes of that interannual variation in space use, we first used two-way ANOVA to search for differences in mean VI between seasons (summer and winter) and between the two populations (Northern Range and Interior). In addition, we used a  $t$  test to assess if VI varied based on the time from reintroduction, i.e., between the first and last five years of study (representing a short and long time after reintroduction, respectively). Subsequently, we ran a set of regression models for which the response variable was  $VI_{i,j}$ . We only included data from the Northern Range of YNP in this analysis, because of better availability of predictor variables in this area of the park. Lack of independence could, in principle, result from a tendency for VI to decrease with an increase in the number of years that separate two estimates of UD. However, this concern is allayed by having observed no significant correlation between the VI indices and the number of years that separated the two UD<sub>s</sub> ( $P = 0.55$ ). To account for multiple observations taken from each pack, we included pack identity in some models as a random effect.

The candidate predictors that we assessed included climatic variables (mean temperature (*temp*, °C) and mean precipitation (*precip*, mm) for each of the two seasons) obtained from the National Biological Information Infrastructure project database of 2011 [note: the NBII was denied funding and went offline in 2012]. We also considered three variables representing population-level properties of the system, *wolf* density, *elk* density, and the *ratio* of wolves to elk. Wolves are counted in YNP each year before the start of the denning season

TABLE 1. Performance of models predicting the volume of intersection during summer (the extent to which intensity of use within a pack's summer territory varied from year to year) for six wolf packs living on the Northern Range of Yellowstone National Park, 1996–2008.

Model	Retained predictors ( $\beta$ s in parentheses)	$K$	df	$\Delta_i$	$w_i$	$R^2$
9	DRUID (−0.04); <u>LEOPOLD</u> (0.10); ROSE (0.06); <u>SLOUGH</u> (−0.17); SWAN (−0.10); <u>leadership</u> (−0.04); litter (0.00)	8	7	0.00	0.9293	0.48
8	DRUID (−0.05); <u>LEOPOLD</u> (0.10); ROSE (0.08); <u>SLOUGH</u> (−0.17); SWAN (−0.07)	6	5	5.15	0.0707	0.43
10	<u>leadership</u> (−0.04); litter (0.00)		5	34.02	0.0000	
4	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.02); litter (0.00); temp (−0.01)	4	4	45.53	0.0000	0.12
3	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.03); litter (0.00)	3	3	46.09	0.0000	0.10
5	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.02); litter (0.00); temp (−0.01); terr (0.00)	5	5	46.28	0.0000	0.13
2	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.03)	2	2	46.44	0.0000	0.07
1	<u>pk-sz</u> (−0.00)	1	1	47.50	0.0000	0.04
6	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.03); litter (0.00); temp (−0.01); terr (0.00); wolf (0.44)	6	6	48.45	0.0000	0.13
7	<u>pk-sz</u> (0.00); <u>leadership</u> (−0.03); litter (0.00); temp (−0.01); terr (0.00); wolf (0.48); precip (−0.01)	7	7	50.76	0.0000	0.13

Notes: AGATE pack is the reference category for *pack ID*. Model 10 treats *pack ID* as a random effect. Predictor abbreviations are: temp (mean temperature, °C); precip (mean precipitation, mm); wolf (wolf density); elk (elk density); ratio (ratio of wolves to elk); litter (litter size); pk-sz (pack size); terr (per capita territory size in km<sup>2</sup>, divided by pack size); leadership (changes in leadership of packs). See *Assessing interannual variability* for additional details. Terms are:  $\beta$ , regression coefficients;  $K$ , number of parameters; df, degrees of freedom;  $\Delta_i$ , difference in Akaike's information criterion adjusted for small sample size, compared to the best-performing model;  $w_i$ , AIC<sub>c</sub> weights. Sample size is 100 for each model. Statistically significant ( $P < 0.05$ ) predictors are underlined.

and in late December from a small aircraft. Estimates for elk density and the ratio of wolves to elk were available only during the winter, because elk counts are typically conducted in the Northern Range from a small aircraft in December or January each year (for details, see Vucetich et al. 2005). Finally, we considered four variables representing properties of individual packs: litter size, pack size (pk-sz), per capita territory size (terr, km<sup>2</sup> divided by pack size), and changes in pack leadership. We did not consider litter as a candidate predictor in the winter models because young wolves can disperse from their natal pack starting in January of their first year (Fuller 1989, Gese and Mech 1991). Because we used VI to quantify year-to-year changes in UDs, each candidate predictor was the absolute value of the difference between two years for that variable. In particular, the leadership variable was the number of alpha wolves that were different between two years (0, 1, or 2). All of the ecological covariates were collected in the process of long-term monitoring of the Northern Range Yellowstone wolf population; see Smith et al. (2004), Vucetich et al. (2011), and Stahler et al. (2013) for details. Packs were included in the regression analyses only if we had data for three or more summers or winters (Appendix A: Table A1). Our data sets included six Northern Range packs for each season. For some models, we also considered pack identity (*pack ID*) as a candidate predictor.

We implemented a model-building strategy designed, in part, to judge the extent to which *pack ID* is necessary for predicting interannual variation in VI. For each season, we built a set of models including, as candidate predictors, all the covariates available for that season (except *pack ID*). We used an automated regression procedure from the “leaps” library of R 3.0.2 (R Development Core Team 2013); see models 1–7 in Table

1. This algorithm uses forward stepwise regression to produce the best-fit (smallest Akaike's information criterion) univariate model, bivariate model, trivariate model, and so on. We compared the performance of these models on the basis of  $P$  values,  $R^2$ , and Akaike's information criterion adjusted for small sample size (AIC<sub>c</sub>). We identified the best model produced by that algorithm and considered a model that included the same predictors, in addition to *pack ID* as a fixed effect. We also considered a model that included only *pack ID* as a fixed effect. We examined each model to ensure that regression assumptions (outliers, normality of the residuals, and homoscedasticity) were met.

Treating *pack ID* as a fixed effect is sensible inasmuch as our interest is to explain variation in VI among the specific packs that were actually observed. However, it is also useful to treat *pack ID* as a random effect, which results in an estimate only of the variance of the intercepts that characterized the packs, rather than estimates of the intercept for each pack. This model corresponds to inferences concerning the influence of other candidate predictor variables, supposing that our sample of packs is randomly selected from among all the packs that could, in principle, have been observed. Considering the influence of a variable when treated as a random effect is important, in a case like this, because doing so sometimes affects estimated values of the coefficients and  $P$  values (Zuur et al. 2009).

## RESULTS

Variation in space use from one year to the next, as quantified by  $VI_{i,j}$ , was highly variable (Fig. 2). The interquartile range was [0.41, 0.59] and the coefficient of variation was 30.6%. A small but statistically significant portion of the observed variation was attributable to differences between seasons (two-way ANOVA,  $F_{1,226} =$

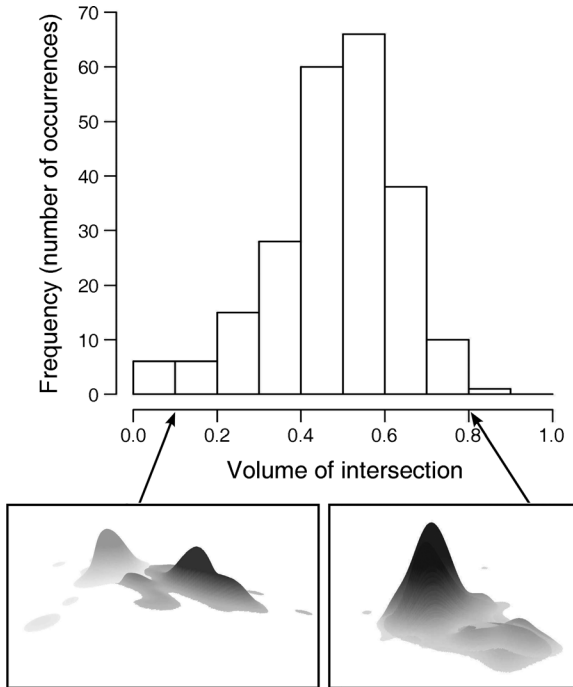


FIG. 2. Frequency distribution of volume of intersection for 15 packs living in Yellowstone National Park between 1996 and 2008. Each estimated volume of intersection represents the extent to which the location and intensity of space use of a pack's territory varied between two years. The lower panels provide a visual depiction of the extent to which utilization distributions (UDs) overlap for given values of volume of intersection. In these examples, the volume of intersection is 0.09 (left panel) and 0.81 (right panel). They represent the winter territories of Druid Peak pack for years 2001 and 2007 (left) and the winter territories of Leopold pack for years 2002 and 2007 (right). The UD plots were created using easting and northing Universal Transverse Mercator (UTM) coordinates in North American Datum 1983 as the  $x$ - and  $y$ -axes, respectively. The  $z$ -axes are based on UD values.

7.70,  $P < 10^{-2}$ ) and differences based on the area of the park where a wolf pack lived ( $F_{1,226} = 9.69$ ,  $P < 10^{-2}$ ). The mean VI was slightly greater during the winter and for Northern Range wolf packs. In other words, wolf space use varied less from year to year in winters and in the Northern Range of YNP (compared to the interior of the park). We found no significant difference based on time from reintroduction ( $t$  test,  $t = 0.31$ ,  $P = 0.76$ ).

*Pack ID*, by itself as a fixed effect, explained 43% of the interannual variation in the intensity of use of each pack's summer territory (model 8 of Table 1; see Fig. 3). The best-fit model indicated that overlap in summer territories was explained by differences between packs (*pack ID*) and differences between years in leadership and litter size. This model also explained 48% of the variation in  $VI_{i,j}$  for summer territories (model 9 of Table 1;  $F$  test,  $F_{7,92} = 12.08$ ,  $P < 10^{-3}$ ; Figs. 3 and 4a). When *pack ID* was excluded, the best model explained 12% of the variation in  $VI_{i,j}$  for the summer territories and indicated that overlap tends to be less between years

during which there are greater differences in pack size, litter size, temperature, and pack leadership (model 4; Figs. 4a and 5a, b). Treating *pack ID* as a random effect did not lead to any model improvement ( $\Delta AIC_c = 34.0$ ; see Table 1). Moreover, the sign and magnitude of the coefficients for the mixed-effect model were very similar to those produced by treating *pack ID* as a fixed effect. In particular, the regression coefficients for these models differed by less than 3% (Appendix B; Fig. B1).

With respect to winter, both the best and second-best models indicated that precipitation and pack size were important predictors of space use (Table 2). There is some evidence that *pack ID* might have been important, but there is a risk that this model (model J) could be overparameterized. Based on the second-best model, overlap in space use tended to be less when there were greater differences in pack size ( $P < 10^{-2}$ ) and precipitation ( $P < 10^{-2}$ ) (model B of Table 2;  $F$  test,  $F_{2,52} = 13.28$ ,  $P < 10^{-3}$ ; Table 2, Figs. 4b and 5c, d). Moreover,  $VI_{i,j}$  was not associated with population-level covariates that one might expect to be important, such as elk density, wolf density, and the ratio of wolves to elk (all  $P$  values  $> 0.3$ ).

## DISCUSSION

Although interannual variation in space use is expected to be a basic feature of a population's ecology, few studies have assessed such variation. This is the first study, to our knowledge, to assess such variation using the volume of intersection index (VI). One of the most straightforward results of this analysis is simply observing basic statistics associated with VI. In particular, of the 15 wolf packs that we observed over a 13-

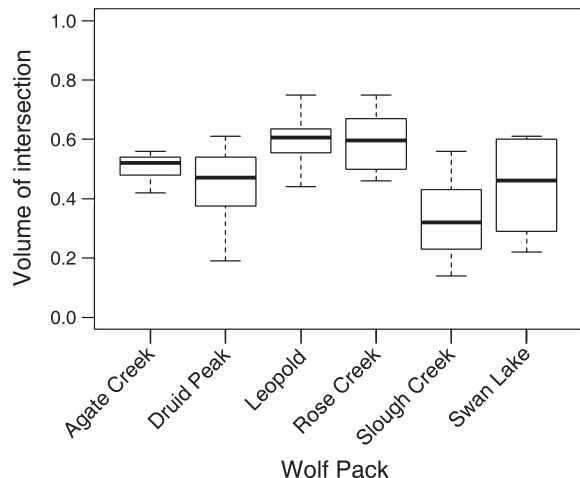
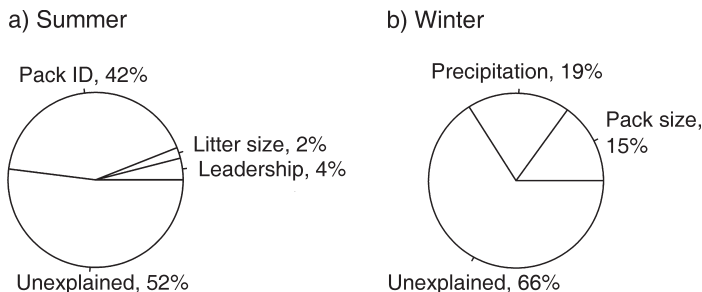


FIG. 3. Volume of intersection, the extent to which the intensity of use within a pack's territory varied between two years, for summer territories of different packs living on the Northern Range of Yellowstone National Park, 1996–2008. These differences among packs are a significant source of total variation in observed volume of intersection (Table 1). Bold bars represent the median, boxes represent the interquartile range, and dotted lines extend to the range of observed data.

FIG. 4. Percentage of variance in volume of intersection, which quantifies the extent to which the intensity of use within a pack's territory varied between two years, explained by various predictors. These results represent the best-fit model for (a) summer territories (model 9 in Table 1) and (b) winter territories (model B in Table 2). The percentage of variance attributed to each predictor is obtained by multiplying the standardized regression coefficient for that predictor by the correlation coefficient between the predictor and volume of intersection (Schumacker and Lomax 2004). For details on the meaning of each coefficient label, see *Materials and methods: Assessing interannual variability*.



year period, the overall mean value of VI was 0.49 (Fig. 2). That is, space use, as represented by utilization distributions, tended to overlap between years by ~50%, suggesting that space use was generally centered on a core area. Moreover, it was not uncommon to observe considerable overlap or very little territorial overlap between years. In particular, ~20% of VI values were greater than 0.7 or less than 0.3 (Fig. 2). Finally, territorial overlap between years was not associated with the period of time separating two UD, suggesting that temporal dynamics in space use did not fluctuate in a gradual, autocorrelated manner. This finding, associated with the lack of difference in VI estimates between beginning and end of the study period, also suggests that space use did not vary as a consequence of recent reintroduction (as noted in other species, e.g., Benson and Chamberlain 2007).

The temporally stable aspects of space use within a territory may be attributable to aspects of the environment that are stable from year to year, such as elevation, slope, aspect, roads, rivers, or vegetation types. That prospect complements the tendency of many habitat studies to focus on such aspects of the environment (e.g., Paquet et al. 1996, Ciucci et al. 2003, Arjo and Pletscher 2004, Oakleaf et al. 2006, Eriksen et al. 2009). Nevertheless, well-established theory suggests that space use should be dynamic, interacting with both density-independent factors, such as climate and resource availability, and density-dependent factors, such as predation and competition (Jonzén et al. 2004, Abrams 2007, Sanchez and Rachlow 2008). To date, the analysis of such relationships is rare (for exceptions, see Kie and Bowyer 1999, Godvik et al. 2009, Ayllón et al. 2013). For this study population, half of the interannual variability in space use appears to have been caused by dynamic aspects of the environment or the population itself. The dynamic aspects of the environment are those characteristics of the environment that may change from one year to the next, e.g., temperature, rather than aspects of the environment that are constant, e.g., slope.

Interannual variability in space use was slightly greater in winter than in summer, and for wolves living on the Northern Range, compared to the Interior. The greater variability observed in winter is probably due to

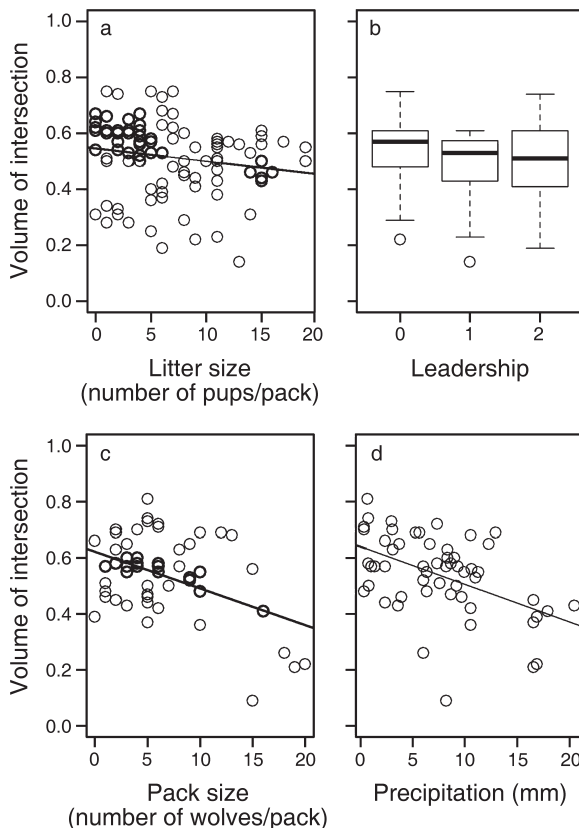


FIG. 5. Influence of various predictors on the volume of intersection index, which quantifies the extent to which the intensity of use within a pack's territory varied between two years. In panels (a), (c), and (d), the x-axes represent differences in the variable value between two years and the black line is a simple linear regression line. In panel (b), each boxplot represents one leadership category (i.e., 0, no differences in leadership between years; 1, one alpha wolf is different between the two years; 2, both alpha wolves are different between years). In (b), bold bars represent the median, boxes represent the interquartile range, and dotted lines extend to the range of observed data. Panels (a) and (b) are derived from model 9 of Table 1 (summer), and panels (c) and (d) are derived from model B of Table 2 (winter).

TABLE 2. Performance of models predicting the volume of intersection during winter, which quantifies the extent to which the intensity of use within a pack's winter territory varied from year to year, for six wolf packs living on the Northern Range of Yellowstone National Park, 1996–2008.

Model	Retained predictors ( $\beta$ s in parentheses)	$K$	df	$\Delta_i$	$w_i$	$R^2$
J	DRUID (–0.02); GEODE (0.12); LEOPOLD (0.09); ROSE (0.14); SWAN (0.03); <u>precip</u> (–0.01); <u>pk-sz</u> (–0.01)	7	7	0.00	0.6089	0.48
B	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01)	2	2	2.45	0.1786	0.34
C	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02)	3	3	3.36	0.1138	0.35
D	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02); <u>elk</u> (–0.01)	4	4	4.78	0.0557	0.36
E	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02); <u>elk</u> (–0.01); <u>terr</u> (0.00)	5	5	6.74	0.0210	0.37
A	<u>precip</u> (–0.01)	1	1	8.06	0.0108	0.24
F	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02); <u>elk</u> (–0.02); <u>terr</u> (0.00); <u>leadership</u> (0.02)	6	6	8.67	0.0080	0.38
G	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02); <u>elk</u> (–0.01); <u>terr</u> (0.00); <u>leadership</u> (0.02); <u>ratio</u> (–6.68)	7	7	11.10	0.0024	0.38
H	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01); <u>temp</u> (0.02); <u>elk</u> (–0.01); <u>terr</u> (0.00); <u>leadership</u> (0.02); <u>ratio</u> (–6.82); <u>wolf</u> (0.35)	8	8	13.80	0.0006	0.38
I	DRUID (–0.13); GEODE (0.09); LEOPOLD (0.02); ROSE (0.03); SWAN (–0.13)	5	5	15.77	0.0002	0.26
K	<u>precip</u> (–0.01); <u>pk-sz</u> (–0.01)		5	26.37	0.0000	

Notes: AGATE pack is the reference category for the *pack ID* dummy variable; see Table 1 for predictor descriptions. Model K is a mixed-effect model with *pack ID* treated as the random effect. Terms are as in Table 1. Sample size for all models is 55. Statistically significant ( $P < 0.05$ ) predictors are underlined.

the different space availability between years with different amounts of precipitation (i.e., different snow cover). Indeed, precipitation was a significant predictor of VI in winter (Table 2). The difference between the two wolf populations may be explained by the Northern Range being a smaller and more stable ecosystem compared to the interior portion of the park. In fact, in the Northern Range, elk are available to the wolf population year-round, whereas the Interior population shifts from a diet based mainly on elk in the summer to a diet based on bison in the winter (Smith et al. 2004).

A large percentage (42%) of interannual variation in space use of Northern Range packs during summer was attributable to consistent differences among packs (Figs. 3 and 4a). These differences could be attributable to unobserved differences between territories in static characteristics of the environment, such as slope and elevation (Milakovic et al. 2011). Moreover, they could represent persistent behavioral differences between packs. That explanation is consistent with having observed a slight influence of changes in pack leadership on variation in space use (Figs. 4a and 5b), with less variation associated with more consistent leadership. This finding is of particular interest because it suggests some kind of individual-level or unique use of a particular area by each pack; heretofore an undiscovered aspect of wolf space use. Additionally, the negative correlation between VI and changes in litter size may be influenced by the presence of multiple litters from different females within the same pack in some years. In these packs, different den sites were used, which may have influenced summer UDs as pack members attended more dispersed den sites (Stahler 2011). These persistent behavioral differences could be attributable to differences in personality and cultural transmission of learned behaviors, as well as composition of social groups regarding breeding structure. Culture, personality, and group composition in social species can each be

important to the fitness of a population in a dynamic environment (Laland and Janik 2006, Cote et al. 2010).

Overlap in winter space use of Northern Range packs was less between years with greater differences in pack size (Figs. 4b and 5c). Pack size represents a process associated with many aspects of wolves' ecology (Vucetich et al. 2004), including density (Appendix C: Fig. C1). The influence of pack size may reflect territorial shifts in response to intraspecific competition with neighboring packs. Recently, Quimby (2013) demonstrated that relative pack size was the most important factor in the odds of a pack being able to successfully displace their opponent. Additionally, the influence of pack size may reflect, in part, larger packs' need to kill more prey. Killing more prey may require packs to use habitat that is less productive, with respect to predation. In YNP, wolves consistently rely on habitat features to enhance their chances to kill prey (Kauffman et al. 2007).

Density-dependent processes (elk and wolf densities) and intraspecific competition (ratio of wolves to elk) were not influential on the temporal dynamics that we analyzed. Density-dependent processes have an important role in wolf survival in the Northern Range (Cubaynes et al. 2014), but do not seem to influence interannual variability in space use. On one hand, we may have failed to capture the influence of predation-related behaviors on space use due to the different temporal scales at which prey density and predator space use were recorded (i.e., one annual winter count vs. several radiotelemetry locations collected between January and March). On the other hand, recent studies support our results by suggesting that prey density is not one of the main factors determining the distribution of predators at a small spatial scale (Milakovic et al. 2011). Instead, predators select habitat features that enhance their ability to encounter and kill prey (Bergman et al. 2006, Kauffman et al. 2007).

Temporal variation in space use during winter tended to be greater between years with greater differences in precipitation, which falls as snow, an abiotic, density-independent factor (Figs. 4b and 5d). The influence of snow probably reflects the tendency for wolves and their prey to concentrate in lower-elevation habitats during years with increased snowfall (Paquet et al. 1996, Ciucci et al. 2003). During those years (likely to become more common in the future due to climate change; Solomon et al. 2007), the reduction of available habitat could deeply affect the dynamics of predator–prey interactions, as well as increase competition among neighboring packs.

The connection between space use and population dynamics is made, in principle, by understanding not only how different kinds of habitat contribute to an organism's fitness in a dynamic environment (e.g., Morris 2003, Jonzén et al. 2004, Abrams 2007), but also how space use varies over relatively long periods of time in real populations and how that variation is associated with other density-dependent and density-independent changes in the environment. The analysis provided here would seem to be a critical, but rarely documented, aspect of understanding this connection between space use and population dynamics.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/13-2116.1.sm>