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Competition, prey, and mortalities influence gray wolf group size

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Abstract

Group living is found in only 10–15% of carnivorans and can shape demographic processes. Sociality is associated with benefits including increased ability to acquire resources, decreased risk of mortality, and increased reproductive success. We hypothesized that carnivore group size is influenced by conditions related to competition, prey, and mortality risk, which should affect benefits and costs of sociality and resulting demographic processes. We evaluated our hypotheses with gray wolves (*Canis lupus*) using a 14-year dataset from a large, heavily managed population in the northern Rocky Mountains, USA. Annual mean group size ranged 4.86–7.03 and averaged 5.92 overall. Most groups were relatively small, with 80% containing ≤8 members. Groups were larger in areas with higher densities of conspecific groups, and smaller where prey availability was low. Group sizes remained largely stable while the population was unharvested or under low-intensity harvest but declined under high-intensity harvest. Results support the hypothesis that as habitat becomes saturated, inclusive fitness may become increasingly important such that subordinates delay dispersal. In addition to direct implications for birth and deaths, conditions related to prey and mortality risk may also influence dispersal decisions. Our work also provided a model to predict group size of wolves in our system, directly fulfilling a management need.

KEYWORDS
benefits and costs, *Canis lupus*, carnivorans, dispersal, gray wolves, group living, group size, sociality

Permanent group living is found in only 10–15% of carnivorans (Gittleman 1989) but is a central feature of the species in which it occurs. Group living transitions the reproductive unit from individuals to social groups, complicating demographic rates and effects of environmental factors and conservation efforts. Given that many carnivores are imperiled or managed heavily by humans (Ripple et al. 2014), a better understanding of sociality can enhance conservation efforts.

Cooperative living among carnivorans confers benefits and costs that influence behavior, demographic rates, and resulting group sizes. Helping related group members can increase an individual's inclusive fitness (Hamilton 1964). Cooperative defense of space can enhance a group's success in defending its territory (Mosser and Packer 2009, Cassidy et al. 2015) and enable offspring to inherit the territory (Lindström 1986). Cooperation can increase the variety of species that can be hunted (Kruuk 1972, Courchamp and Macdonald 2001), hunting success (Creel and Creel 1995), and ability to acquire food through kleptoparasitism (Courchamp and Macdonald 2001, Lehmann et al. 2016). Group living can enhance survival when group members detect and repel predators (Clutton-Brock et al. 1999, Courchamp and Macdonald 2001, Lehmann et al. 2016), rescue group members after capture (Rood 1983), or guard and provision injured or sick group members (Rood 1986, Almberg et al. 2015). A key benefit can also be enhanced reproductive success through cooperation in rearing young (Clutton-Brock et al. 1999, Macdonald and Sillero-Zubiri 2004, Mosser and Packer 2009, Creel and Creel 2015, Ausband et al. 2017). Conversely, sociality often heightens competition for resources and reproduction. Per capita food intake may decrease as group size increases or after exceeding an optimum group size (Peterson and Ciucci 2003, Vucetich et al. 2004). Lower-ranked individuals may receive fewer food resources and suffer greater mortality as a result (Mech 1999, Courchamp and Macdonald 2001, Holekamp et al. 2007, Creel and Creel 2015). Subordinate individuals may be prevented from reproducing (Schneider and Kappeler 2014, Ausband 2018). Additionally, larger groups may decrease confidence of paternity for males (Ausband 2018), and certain helpers may reduce offspring survival (Ausband et al. 2017).

Competition is likely a primary factor influencing group size in social carnivorans. Competition may negatively affect births and deaths by reducing per capita resources in an area and increasing conspecific aggression. Intergroup competition, however, likely also influences immigration and dispersal (i.e., among groups or to establish new groups; Emlen 1982*a*, 1994, 1995). An increase in densities of nearby groups may signal less space for new home ranges and greater risk of conspecific mortality while dispersing, causing delayed dispersal and a positive effect on group size. Individuals that delay dispersal and help relatives raise offspring may also benefit from inclusive fitness (Hamilton 1964; Emlen 1982*a*, *b*, 1995). Birth rates can rise if delayed dispersal causes multiple group members to produce litters (Ausband 2018). Additionally, groups may be more accepting of immigrants at high group densities, when territorial disputes may increase and larger groups have greater odds of winning confrontations (Mosser and Packer 2009, Cassidy et al. 2015). Accordingly, group size may increase with competition through effects on dispersal, immigration, or multiple breeders, even if birth rates fall or mortality rates rise (Table 1).

Prey may also influence demographic rates and resulting group size in carnivorans. Birth rates may fall and death rates rise if prey acquisition falls below per capita requirements (e.g., in terms of kg of food/individual, prey biomass on the landscape, or number of individuals on the landscape), as observed, for example, in gray wolves (*Canis lupus*) in relation to prey biomass (Fuller et al. 2003). If group members cannot meet their food requirements, dispersal is likely optimal (Gese et al. 1996, Peterson and Ciucci 2003). The opposite is likely to occur with greater access to food resources by increasing the group sizes that can be maintained, causing group size to positively correlate with prey abundance and availability (Table 1; Fuller et al. 2003, Mech and Boitani 2003).

Mortalities directly decrease group size but may also have wider effects. Deaths of parents or helpers may lead to further deaths of dependent young (Creel and Creel 2015, Ausband et al. 2017). Survivors may also have more

TABLE 1 Hypothesized relationships between group size and variables related to competition, prey, mortality, and mortality risk for wolves in Montana, USA, 2005–2018. We considered hypotheses to have support when 90% confidence intervals did not overlap zero, as determined by variables included in the top model or through secondary analyses of models with single fixed effects (denoted by *). Supported hypotheses included H_1, H_3, H_{4b}, and H_{4d}

Variables hypothesized to influence group size	Expected relationship	β	CI_{lower}	CI_{upper}
Competition				
Density of groups	H_1: +	0.080	0.038	0.122
Prey				
Prey abundance—summer ungulate density	H_{2a}: +	0.024*	−0.018	0.065
Prey abundance—winter ungulate density	H_{2b}: +	0.015*	−0.024	0.053
Prey availability (terrain ruggedness)	H_3: −	−0.045	−0.085	−0.005
Mortalities and mortality risk				
Harvest mortality density	H_{4a}: −	−0.015	−0.065	0.035
Control removals	H_{4b}: −	−0.061	−0.097	−0.027
Intensity of harvest management (restricted)	H_{4c}: −	−0.084	−0.177	0.008
Intensity of harvest management (liberal)	H_{4d}: −	−0.188	−0.291	−0.083
Human density	H_{4e}: −	0.032*	−0.002	0.066
Density of low-use roads	H_{4f}: −	0.000*	−0.040	0.040

difficulty hunting prey (Creel and Creel 1995), defending territories (Cassidy et al. 2015), and assisting injured or sick group members (Almberg et al. 2015). Dispersal might increase to avoid risks of death or in response to reduced inclusive fitness benefits (Emlen 1995). Smaller groups would be the outcome of these mortalities and behavioral responses (Table 1).

Although demographic rates within carnivore groups are difficult and costly to measure in wild populations, changes to group sizes can provide evidence of how competition, prey, and mortalities affect groups. Understanding these effects is arguably particularly important in heavily managed carnivore populations. For example, Montana, USA, exemplifies the future of large carnivore management, whereby gray wolves and other large carnivores must coexist on human-dominated landscapes and are heavily managed through harvest and control removals (i.e., removals in response to livestock depredations). Wolves generally live in groups composed of a dominant breeding pair and their subordinate offspring from multiple years, along with immigrants occasionally adopted into the group (Mech and Boitani 2003). Groups defend territories with variable degrees of overlap (Uboni et al. 2015). Like many large carnivores, wolves were extirpated from most of the contiguous United States in the twentieth century. Following Endangered Species Act protections, recolonization, and reintroductions into the northern Rocky Mountains, USA, wolf numbers increased and wolves were successfully delisted in Montana in 2009 and 2011 (with a brief re-listing in 2010 due to court challenges; Fritts et al. 1997, Bradley et al. 2014). Delisting returned management to the state, and harvest seasons were carried out in 2009 and 2011 onward.

Throughout wolf recovery, Montana Fish, Wildlife and Parks (MFWP) maintained intensive monitoring efforts to estimate group sizes, but high costs of monitoring caused these efforts to wane after 2018. Since 2007, MFWP has used an occupancy model and average observed territory size to estimate group abundance (calculated as area occupied divided by mean territory size; Miller et al. 2013, Rich et al. 2013). Total wolf abundance was then calculated as the number of estimated groups multiplied by the average observed group size each year (Inman et al. 2019). Absent annual monitoring data on group sizes, total wolf abundance could be estimated with a model that predicts group size. A useful model would predict group sizes with minimal data given the costs and difficulties of monitoring an elusive large carnivore over vast areas.

Our objective was to understand factors affecting group size for gray wolves, using Montana's portion of the northern Rocky Mountain wolf population as a study system. Additionally, we sought to develop a model to predict wolf group size in Montana. We hypothesized that wolf group size is influenced by factors associated with competition, prey, mortality, and mortality risk (Table 1) based on the reasons outlined above. We expected that intergroup competition could be represented by intergroup density, and prey abundance by ungulate monitoring data. We also expected rugged terrain could decrease availability of ungulates because wolves are coursing predators (Peterson and Ciucci 2003) who may make more kills at lower elevations (McPhee et al. 2012) and have lower hunting success in rugged terrain (Rich et al. 2012). We expected mortalities and mortality risk could be represented using data for harvest densities, control removals, and intensity of harvest management. We also hypothesized greater densities of humans and low-use roads (which are often used by recreationists) could mean more hunters and mortalities, plus greater perceived mortality risk given the natural wariness of wolves towards humans (Whittington et al. 2004, Hebblewhite and Merrill 2008, Latham et al. 2011). After testing our hypotheses about effects of competition, prey, and mortality risk on Montana's wolf population, we adapted our top model into a predictive model to assist MFWP in estimating wolf abundance.

STUDY AREA

Our study area comprised Montana (380,800 km^2) where elevations ranged from 550–3,902 m (Foresman 2001). During our study from 2005–2018, wolf packs primarily occupied western Montana (Figure 1; Inman et al. 2019). In the Northern Rockies Ecoregion (epa.gov/eco-research/ecoregions, accessed 8 Jul 2019) of northwestern Montana, dense forests covered rugged, mountainous terrain. This transitioned to glaciated, higher-elevation terrain of the Canadian Rockies Ecoregion, and farther east, to level, rolling terrain and seasonal wetlands and ponds of the Northwestern Glaciated Plains. In southwestern Montana, the partially glaciated, mountainous Idaho Batholith transitioned eastward to rolling foothills and rugged mountains of the Middle Rockies. Eastward, the semiarid plains of Northwestern Great Plains were interspersed with breaks and forested highlands. West of the Continental Divide, climate was characteristic of northern Pacific coastal climates, whereas east of the Divide was semi-arid and continental. White-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus canadensis*), and moose (*Alces alces*) comprised the primary prey for wolves. Other large carnivores included coyotes (*C. latrans*), American black bears (*Ursus americanus*), grizzly bears (*U. arctos*), and mountain lions (*Puma concolor*). Montana's human population was approximately 934,500 in 2005 and 1,062,000 in 2018 (census.gov, accessed 18 Jan 2019), and land use included extensive public lands, rangelands, and croplands. In 2009 and 2011–2018, harvest through hunting and trapping caused 72–295 wolf mortalities ($\bar{x}$ = 211) per harvest season, which began in September and ended each November (2009), February (2011 and 2012), or March (2013 onward). Agency control removals for livestock conflicts removed 28–128 wolves per year from 2005–2017.

METHODS

Data

Wolf specialists from MFWP monitored groups through radio-tracking, camera-trapping, and aerial surveys each year from 2005–2018 to verify group presence, count group members, and estimate year-end group sizes (fwp.mt.gov, accessed 18 Jan 2019). We retained for analysis only good quality counts, which were from groups documented multiple times each year using trail cameras, visual sightings, or track surveys. Wolf specialists

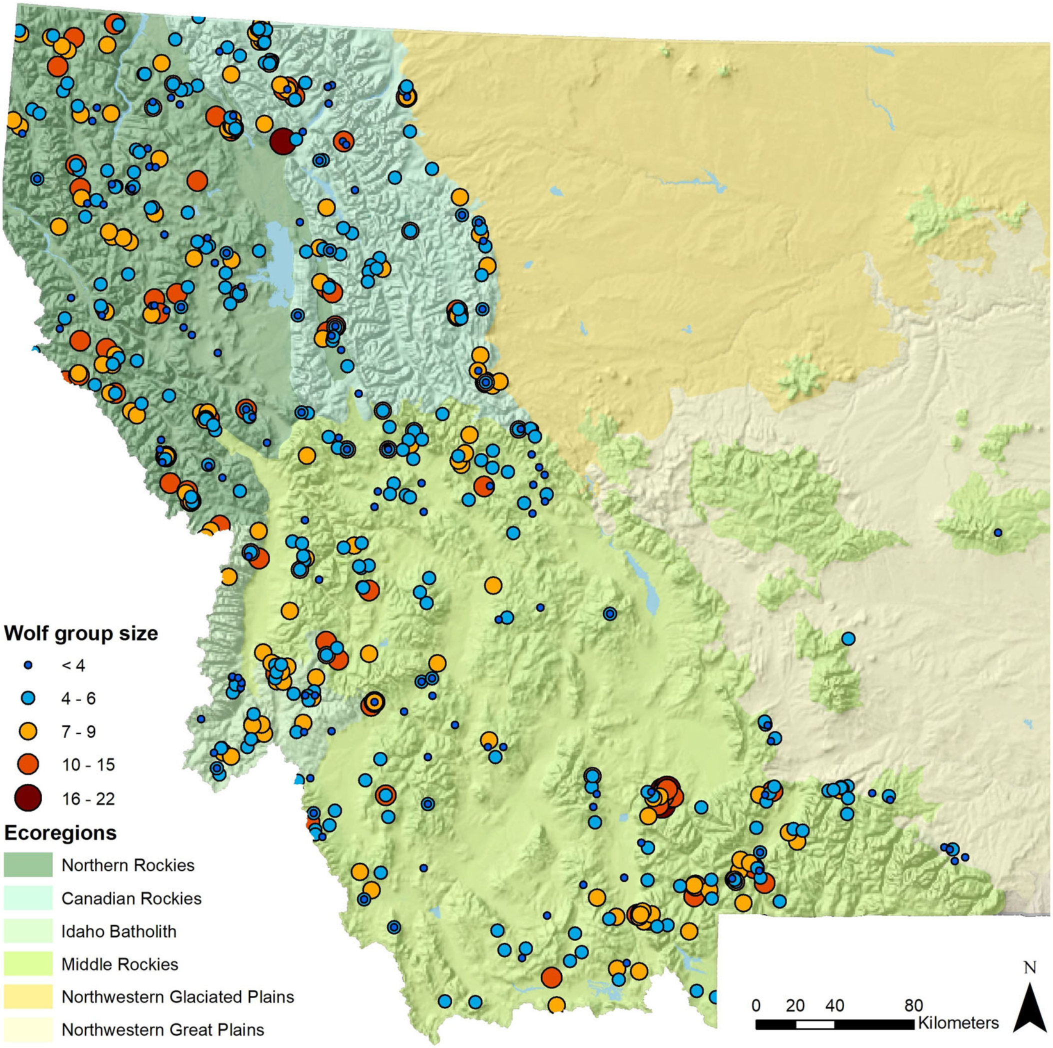

FIGURE 1 The study area encompassed wolf distribution in Montana, USA. Wolves primarily occupied western ecoregions (the Northern Rockies, Idaho Batholith, Canadian Rockies, and Middle Rockies). Wolf group sizes for 2005–2018 are shown and demarcate the group's territory centroids

estimated an annual territory centroid for each group using radio-collared wolves, field surveys, and expert knowledge. We tested for spatial autocorrelation of centroid distances and group size for each year using Moran's *I* with package spdep (Bivand and Wong 2018).

We estimated local conditions related to competition, prey, and mortality risk using relevant spatial data and program R (R Core Team 2020) with R packages raster (Hijmans 2020) and tidyverse (Wickham et al. 2019), as follows. In each case, we measured the mean value of the covariate within the local vicinity of each group's annual territory centroid (defined as 12.41 km around the centroid, based on the 484-km^2 geometric mean territory size for wolves in Montana, 2014–2019; Sells et al. 2021).

We represented competition as density of groups. We first created annual rasters of intergroup densities using annual territory centroid locations and the kernel smoothed intensity function in spatstat (Baddeley et al. 2015) with sigma set to 25 km to allow for variable territory sizes around the known centroids. Within each group's local vicinity, for each year we then measured densities of groups per 1,000 km^2.

To represent prey abundance, we used seasonal density indices for ungulates (deer, elk, moose) across western Montana (Sells et al. 2021). We calculated preliminary seasonal indices for deer and elk as long-term, species-specific density indices per km^2 using delineated summer or winter habitat (fieldguide.mt.gov, accessed 18 Nov 2018) and the most recent 10-year mean abundances per MFWP administrative region (fwp.mt.gov, accessed 18 Nov 2018; such estimates were considered to be most reliable across our large spatiotemporal scales). To make more locally specific estimates of ungulate densities, we incorporated local relative catch per unit effort (CPUE, which often correlates to prey abundance; Dusek et al. 2006, Rich et al. 2012) by creating a local adjustment factor (*L*) as the 10-year mean CPUE (number of males harvested/hunter days from 2008–2017; fwp.mt.gov, accessed 18 Nov 2018) within each hunting district divided by the regional 10-year mean CPUE. We multiplied *L* by the preliminary density index to calculate a final density index for each species and seasonal habitat; *L* adjusted the density index upward where CPUE was relatively high and decreased it where low. Environmental conditions that influence hunting success are expected to be more similar within MFWP regions than at the statewide level. Therefore, a relatively high CPUE is expected to indicate a higher ungulate abundance compared to nearby districts with lower CPUE. We estimated seasonal moose indices by dividing estimated moose abundance per hunting district (N. J. DeCesare, MFWP, unpublished data) by the area of summer and winter habitat. Within each group's local vicinity, we measured mean estimated summer and winter densities of ungulates (deer + elk + moose).

We calculated our index for prey availability (terrain ruggedness) using the vector ruggedness measure (Sappington et al. 2007) with spatialEco (Evans 2018) and elevation data from package elevatr (Hollister and Shah 2017). Within each group's local vicinity, we then estimated mean terrain ruggedness.

For mortalities and mortality risk, we first estimated annual densities of harvest mortalities/1,000 km^2 using reported locations of harvested wolves and the kernel smoothed intensity function in spatstat (Baddeley et al. 2015) with sigma set to 25 km. Group-specific control removals were recorded by MFWP. We classified intensity of harvest management as hunting seasons with no harvest (≤2008 and 2010), restricted harvest (2009 and 2011; when statewide harvest was limited by a quota, seasons were shorter, bag limits were low, and trapping was prohibited), and liberal harvest (2012 on, when statewide harvest quotas were removed, seasons were longer, bag limits were higher, and trapping was allowed). Within each group's local vicinity, we measured mean density of humans (humans/$mile^2$) using 2010 census data and mean density of low-use roads (km/km^2) using the most recent road dataset (geoinfo.msl.mt.gov, accessed 18 Mar 2019).

Hypothesis tests

We tested our hypotheses using generalized linear mixed-effects models (family = Poisson) with R package lme4 (Bates et al. 2015) and AICmodavg (Mazerolle 2020). We designed 10 competing models (Table 2; Appendix A) to focus on competition, prey, or mortality risk, and their combined effects. We included variables for mortalities (i.e., density of harvest mortalities, number of control removals, and intensity of harvest management) in each model because these should directly influence group size. We also added a random effect for group identity to each model. We identified the most supported models using the Akaike's Information Criterion (AIC; Burnham and Anderson 2002) with a cut-off of 2 ΔAIC (Anderson et al. 2001) for supported models. Model variables were centered and scaled, with resulting units representing standard deviations from the mean. We considered a hypothesis to have support if 90% confidence intervals of the coefficient estimate (ß) excluded zero. We transformed variables to original units to display effect plots for each variable in the top model. For covariates not in the top model, we tested our hypotheses using models with a single fixed effect for the covariate of interest. We displayed results using tidyverse (Wickham et al. 2019), jtools (Long 2020), effects (Fox and Hong 2009), and cowplot (Wilke 2020).

TABLE 2 Support for models of wolf group size in Montana, USA, 2005–2018. Models focused on different combinations of factors hypothesized to influence group size. All models included mortality variables of harvest mortality density, harvest intensity, and control removals

Model	Model focus	K[a]	AIC[b]	ΔAIC	AIC weight	Log likelihood
7	Competition + prey availability	8	3,076.03	0.00	0.54	−1,530.01
1	Competition	7	3,077.49	1.46	0.26	−1,531.74
9	Competition + mortality risk	9	3,079.83	3.80	0.08	−1,530.91
6	Competition + prey abundance	9	3,081.01	4.98	0.05	−1,531.50
10	Competition + prey[c] + mortality risk	11	3,081.02	4.99	0.04	−1,529.51
2	Winter prey abundance	7	3,084.59	8.56	0.01	−1,535.29
5	Mortality risk	8	3,084.59	8.56	0.01	−1,534.29
3	Summer prey abundance	7	3,084.60	8.57	0.01	−1,535.30
4	Prey	9	3,087.49	11.47	0.00	−1,534.75
8	Prey + mortality risk	11	3,088.71	12.68	0.00	−1,533.36

[a] Number of estimated parameters for the model.

[b] Akaike's Information Criterion.

[c] Includes prey abundance and availability unless otherwise specified.

Predictive model

We adapted our top identified model into a predictive model. To maximize parsimony and minimize required monitoring effort, we first dropped any variables with confidence intervals overlapping zero. Because obtaining group centroids through monitoring is costly, we used the spatially explicit mean group density observed from 2005–2018 as an index to long-term density trends. Because control removals were group-specific and this level of detail may not always be available, we divided Montana into a grid of 600-km^2 cells and summarized annual control removals reported in each cell. To capture additional environmental effects, we added a covariate representing the ecoregion in which a territory centroid fell (Figure 1). We included a random effect for the 600-km^2 grid cell in which the territory centroid fell in place of a group-specific random effect to account for repeated observations among years. We then refit the model with its updated parameters.

To test our model's predictive capacity, we compared predicted versus observed annual mean group size. To generate predicted group sizes, we measured mean values for model covariates in each 600-km^2 grid cell. We next obtained from MFWP's wolf occupancy model (Inman et al. 2019) annual, cell-specific probability of occupancy, pr(occupancy), for 2007–2018. For each year we applied the model covariates to cells with ≥0.5 pr(occupancy) and then calculated mean group size predicted in these cells (which were more likely to actually contain wolf groups). For 2005 and 2006 (when occupancy data were not available), we predicted group size per cell known to have a group. Finally, we estimated a linear regression of predicted annual mean group sizes versus those observed from monitoring. If the regression slope estimate's 95% confidence interval overlapped 1.0 (Rich et al. 2012), we considered the model to reliably estimate annual mean group size.

RESULTS

From 2005–2018, MFWP monitored 46–152 groups/year, totaling 1,531 group-years. Of these, 26–68 groups/year had good quality counts, yielding 660 group-years from 220 groups for analysis. Annual mean group size ranged from 4.86–7.03 and averaged 5.92 overall (Figure 2). Most groups were relatively small, with

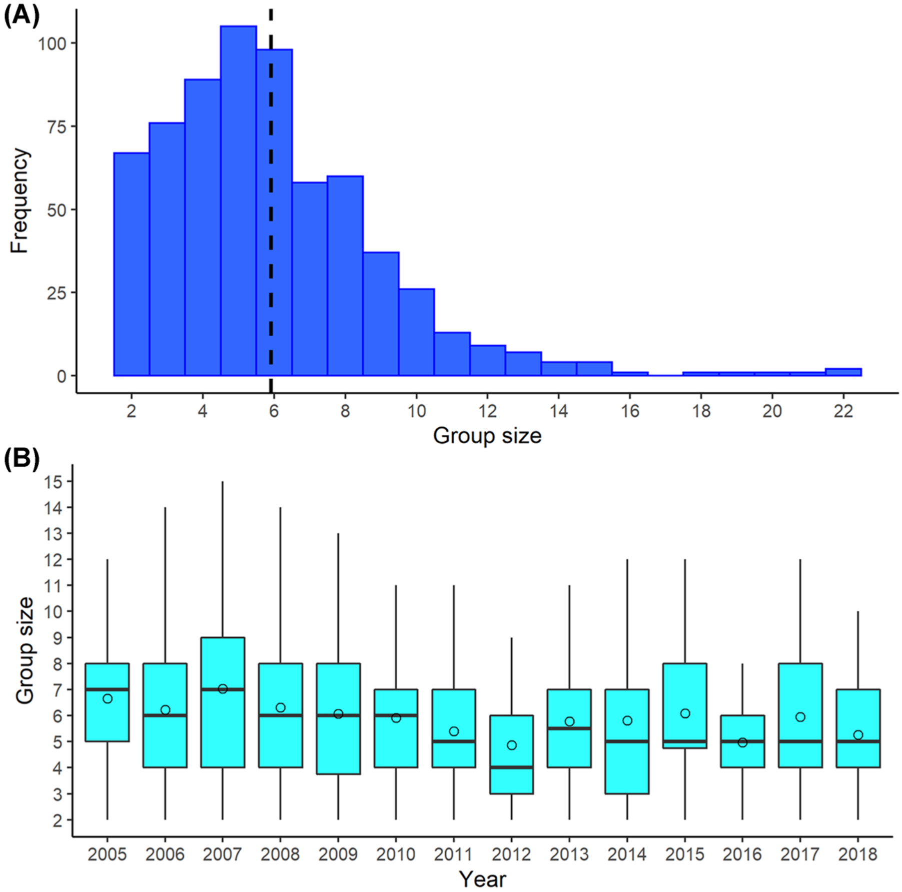

FIGURE 2 Observed wolf group sizes in Montana, USA, 2005–2018. Panel A: group sizes ranged 2–22, with a mean of 5.92 (dashed line). The 50% interquartile range was 4–8 members per group. Panel B: group sizes varied slightly by year. Boxplot whiskers extend 1.5 times the interquartile range, center lines are median values, and points are mean values

80% containing ≤8 members. Group size was not spatially correlated (mean annual Moran's I = − 0.017, range = −0.108–0.036).

Two models had support (Table 2; Appendix A). The top model focused on competition and prey availability (Figure 3; Table 1) and revealed that group size increased with density of groups and decreased with greater terrain ruggedness (Figure 4). Control removals and liberal harvest had negative effects, whereas restricted harvest had an uncertain effect. Group size had no clear relationship with harvest mortality density. The second-ranked model omitted ruggedness and otherwise had similar effects. Covariates excluded from the top models (densities of prey, humans, and roads) had no measurable effects on group size (Table 1).

The predictive model adapted from our top model likewise revealed a positive relationship of group size with group density, and negative relationships with ruggedness, harvest intensity, and control removals (Table 3). Group sizes varied slightly by ecoregion; compared to the Northern Rockies, groups were smaller in the Idaho Batholith and larger elsewhere in western Montana. The model reliably estimated annual mean group size (Figure 5); a linear regression of annual mean observed versus predicted group sizes included 1.0 (ß = 0.81, 95% CI = 0.319, 1.307, R^2 = 0.52, $F_{1,12}$ = 12.84, P = 0.004).

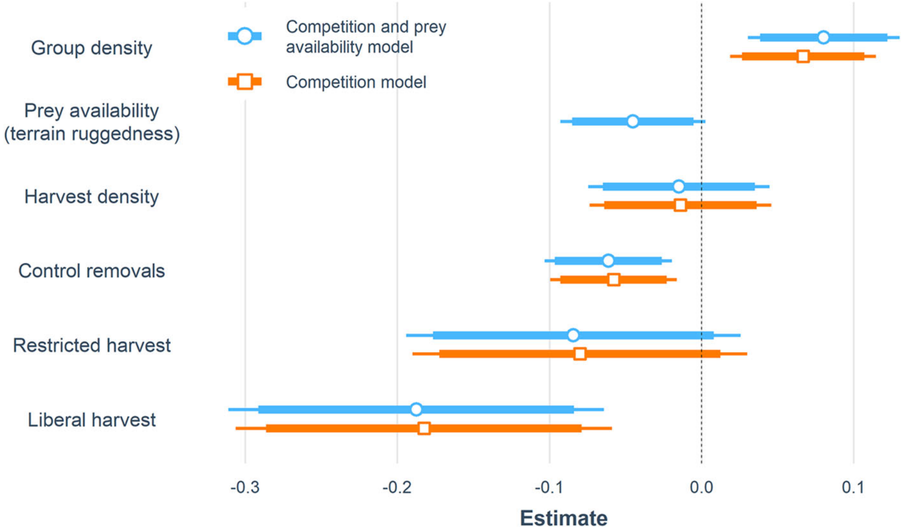

FIGURE 3 Top models for wolf group sizes included variables related to competition, prey, and mortality risk for wolves in Montana, USA, 2005–2018. Thicker line segments represented 90% confidence intervals, full lines the 95% confidence intervals, and points the mean estimates

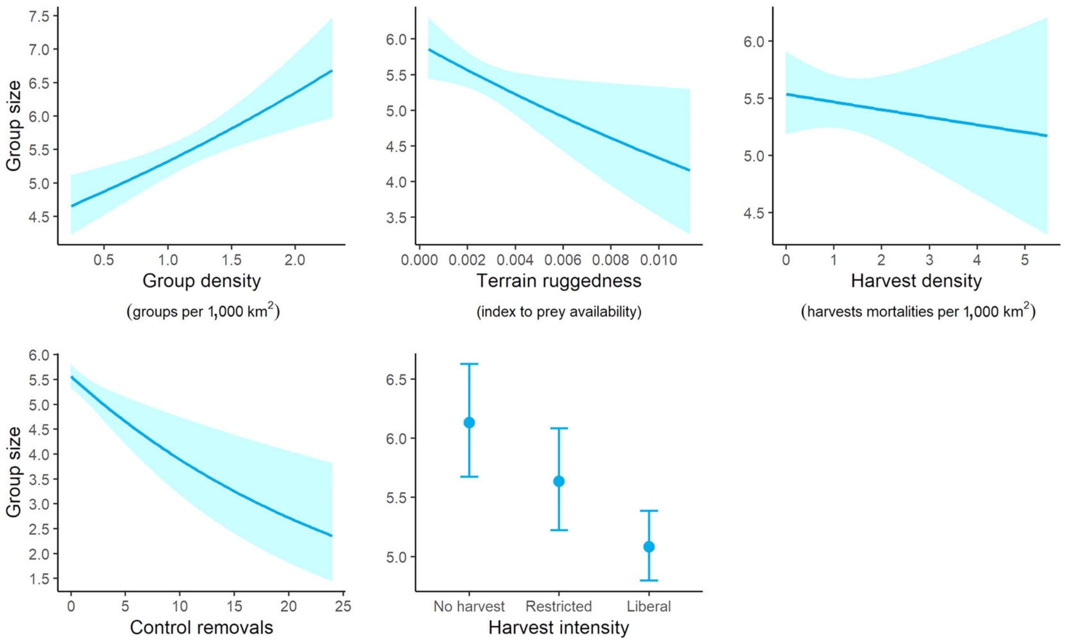

FIGURE 4 Effects plots for variables in the top model for wolf group size, as measured for wolves in Montana, USA, 2005–2018. Variables are on their original scales, and in each plot panel, remaining variables are held to their mean values. Confidence intervals are shown at their 90% levels

TABLE 3 Predictive model for wolf group sizes in Montana, USA, 2005–2018. Variables and their 95% confidence intervals are reported on the log scale. Input data were not transformed for this model

Coefficients	Estimate	Lower CI	Upper CI
Intercept	1.56	1.324	1.803
Mean group$_{\text{density}}$	0.44	0.259	0.624
Ruggedness	−67.28	−99.661	−34.892
Harvest intensity$_{\text{restricted}}$	−0.06	−0.158	0.043
Harvest intensity$_{\text{liberal}}$	−0.18	−0.257	−0.100
Grid-level control$_{\text{removals}}$	−0.03	−0.049	−0.005
Ecoregion: Idaho Batholith	−0.06	−0.245	0.120
Ecoregion: Middle Rockies	0.04	−0.095	0.166
Ecoregion: Canadian Rockies	0.13	−0.019	0.286
Ecoregion: Northwestern Glaciated Plains	0.03	−0.327	0.390
Ecoregion: Northwestern Great Plains	0.00	−0.320	0.317

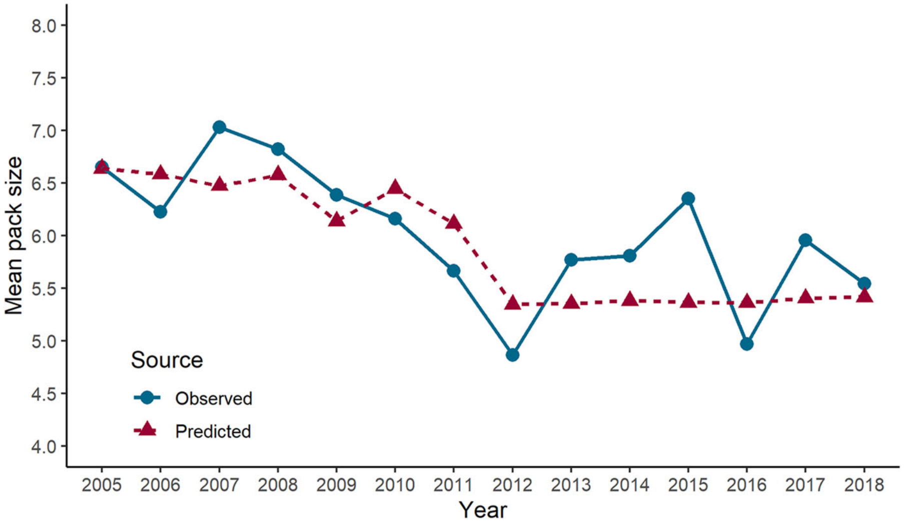

FIGURE 5 Predicted annual mean group sizes reflected observed mean group sizes for wolves in Montana, USA, 2005–2018. Predictions were from the predictive model developed in this study

DISCUSSION

We investigated factors influencing group size in gray wolves living in a large, heavily managed population. Analysis of a long-term monitoring dataset revealed that wolf groups were larger in areas with higher densities of conspecific groups, and smaller with both low prey availability and more human-caused mortality. Results contribute evidence that social carnivores may use nearby group densities as cues about the benefits and costs of delaying dispersal in response to increased competition for space. Results also contribute evidence that these social carnivores experience depressed group sizes at higher mortality rates but no appreciable change in group size at a relatively low harvest intensity. Additionally, a predictive model for group size developed from this work directly fulfills a management need.

A positive relationship between the density of groups and group size supported the hypothesis that nearby group densities influence group size (Figure 4; Table 1). Under this hypothesis, we expected that even if increased competition caused detrimental effects on births or deaths, group size would increase through delayed dispersal. Although patterns we observed may have also been driven by multiple breeders per group, relatively small group sizes make this unlikely (Ausband 2018). Our results support Emlen's (1982*a*) hypothesis that group living evolved as a result of delayed dispersal in response to habitat saturation. Similarly, declines in rates of carnivore dispersal have been associated with wolf population increases (Jimenez et al. 2017), greater numbers of neighboring prides of lions (*Panthera leo*; VanderWaal et al. 2009), and saturated habitats for Ethiopian wolves (*C. simensis*; Sillero-Zubiri et al. 1996). As habitat becomes saturated, inclusive fitness may become increasingly important such that subordinates decide to stay and help rather than risk injury or death from encounters with conspecifics during dispersal (Emlen 1982*a*, *b*, 1995). We expect that local group densities are cues to the costs and benefits of staying versus leaving, and that these densities could be detected through direct interactions, signals such as scent marks or howling, and pre-dispersal forays (Messier 1985, Mech and Boitani 2003). Such forays were evident among radio-collared individuals in our study area (S. N. Sells, University of Montana, unpublished data). Because a group's competitive ability and success in territorial defense increases with group size (Cassidy et al. 2015, Sells and Mitchell 2020), at high group densities groups may be more accepting of both delayed dispersal by subordinates and immigrants seeking to join the group.

Wolf groups were smaller where food availability was low (Figure 4; Table 1), indicating that advantages of sociality likely decrease when food availability declines. We assumed that terrain ruggedness was a credible index to prey availability (Peterson and Ciucci 2003, McPhee et al. 2012, Rich et al. 2012), and although its relationship with group size could have been related to other factors, ruggedness had minimal correlation with other variables. Contrary to our index for prey availability, prey abundance was not associated with group size. Higher-resolution data may show that prey abundance positively correlates with group size in Montana given that in similar systems, wolf densities, litter sizes, and pup survival correlate with prey biomass (Fuller et al. 2003) and availability (Mech et al. 1998). Pack size does not, however, correlate with prey biomass at continental scales (Fuller et al. 2003) or with measures like ungulate occupancy at smaller scales (Kittle et al. 2015). Instead, primary prey body size may correlate with group size, possibly because larger groups have greater success in capturing larger prey (Fuller et al. 2003, MacNulty et al. 2014). In contrast, prey abundance appears to have greater effects on territory size (Kittle et al. 2015; Sells and Mitchell 2020; Sells et al. 2021, 2022). Adding further complexity, social canids may disperse at greater rates when prey abundance is low (Messier 1985, Peterson and Page 1988, Gese et al. 1996, Fuller et al. 2003). Observed relationships between prey and carnivore group sizes may accordingly be an outcome of not only births and deaths but dispersal once costs of group living (i.e., insufficient food resources) outweigh benefits of staying (Ekman et al. 2004).

Mortality and mortality risk had variable effects on wolf group sizes (Figure 4; Table 1). Wolf group size declined with more control removals. In contrast, local densities of harvest, humans, and low-use roads had no measurable effects. Lower intensity of harvest management in 2009 and 2011 also had a limited, uncertain effect on group size, which could have been an outcome of restrictive regulations (which entailed statewide quotas, lower bag limits, and no trapping) or a recovery year absent harvest. More liberal harvest regulations (entailing no quotas, higher bag limits, and both hunting and trapping) had measurable effects, however, from 2012 on. In northern Alaska, USA, transient wolves appeared to constitute relatively large portions of harvest by humans, leaving group size relatively unaffected at low levels of harvest through potential effects on dispersal decisions; however, populations declined at higher harvest rates (Adams et al. 2008). Similarly, wolf group sizes in southern Alaska declined at higher harvest rates (Peterson et al. 1984). Mortalities may not only directly decrease group size but depress survival of remaining group members (e.g., via higher mortality of young after the death of a parent or helper), as evidenced in Idaho, USA (Ausband et al. 2017). Wolf groups are also more likely to disband after loss of dominant individuals (Brainerd et al. 2008). Dispersal in response to greater harvest intensity would serve to replenish breeder or territory vacancies quickly, which in turn could lead to more compensation under intensive harvest than may otherwise be expected. We suspect effects on dispersal and take of transient wolves helps explain the apparent overall stability of some harvested wolf populations like ours despite years of intensive harvest (Fuller et al. 2003, Adams et al. 2008, Inman et al. 2019).

Data for group-specific demographic rates are rarely available, especially where large carnivores coexist alongside humans outside protected reserves. Montana provided a large, long-term monitoring dataset of group sizes to test our hypotheses. Although smaller groups could conceivably be more difficult to find and count, 80% of groups monitored contained ≤8 group members and 51% had ≤5 members (Figure 2). Undetected groups would lead to locally underestimated densities and likely weaken measurable relationships with group size. We expect additional data would also reveal sex-specific costs and benefits of sociality. Previous work reported equal dispersal rates among male and female yearling wolves but male-biased dispersal among adults (Jimenez et al. 2017). If adult males decrease pup survival (Ausband et al. 2017), groups should pressure males to disperse. Females may conversely experience greater benefits from staying in the natal group (e.g., by obtaining a secondary breeding position; Ausband 2018). Furthermore, it appears females more often rely on forming new territories rather than immigrating into groups (Jimenez et al. 2017), which would place greater benefits on delaying dispersal when high group densities make it too costly to carve out a new territory.

MANAGEMENT IMPLICATIONS

Our findings can assist managers, including where gray wolves continue expanding their current range. Given that groups were generally smaller where group densities were low, smaller groups might be expected in areas with recent recolonization or high mortality. If this relationship is caused in part by dispersal, these same areas may see relatively rapid colonization. After the territory mosaic begins to fill in, group size is expected to generally increase at the same time territories are expected to compress (Sells and Mitchell 2020; Sells et al. 2021, 2022), which may produce relatively high population densities. Managers can also expect wolf groups to be smaller where prey availability is reduced and in areas of higher harvest intensities. In contrast, a lower harvest intensity may not substantially influence mean group size in similar systems.

Our approach provided the framework for a predictive model for mean group size. Despite omitting within-group demographic data, our model accurately predicted annual mean group size for wolves in Montana. The model can be used alongside a recently developed mechanistic territory model (Sells and Mitchell 2020; Sells et al. 2021, 2022) and existing occupancy models (Miller et al. 2013, Rich et al. 2013) to estimate wolf abundance with limited data. Previously, this occupancy-based approach relied on intensive monitoring to estimate group sizes each year. This is challenging, time-consuming, and costly. Intensive monitoring of group sizes is unviable when the number of known groups far exceeds 100 separate groups spread across an estimated ≥62,000-km^2 area. Failure to accurately estimate group sizes could bias abundance estimates low or high, whereas our model can help predict annual mean group sizes to improve reliability of wolf abundance estimates. Our predictive model can therefore directly inform management of a large carnivore population.

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CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

Wolves captured by MFWP for radio-collaring were anesthetized and handled in accordance with MFWP's biomedical protocol (Montana Fish, Wildlife and Parks 2005), guidelines from the Institutional Animal Care and Use Committee for the University of Montana (AUP number 070–17), and guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

DATA AVAILABILITY STATEMENT

Data and R code used in the analyses for wolf group sizes can be found at Zenodo (Sells 2022).

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SUPPORTING INFORMATION

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APPENDIX A: MODEL SET AND RESULTS

We grouped models by their main focus. All models included a random effect for group identity. Models also all included mortality variables (density of harvest mortalities, number of control removals, and intensity of harvest management) because mortalities directly influence group size. No variables were overly correlated (>0.7 Spearman's rank correlation; Dormann et al. 2013). Two models had support (Table 2; Table A1).

1. Competition most influential: $\text{group}_{\text{density}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
2. Winter prey abundance most influential: $\text{ungulate}_{\text{winter}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
3. Summer prey abundance most influential: $\text{ungulate}_{\text{summer}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
4. Prey abundance and availability most influential: $\text{ungulate}_{\text{winter}} + \text{ungulate}_{\text{summer}} + \text{ruggedness} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
5. Mortality risk most influential: $\text{roads}_{\text{low-use}} + \text{human}_{\text{density}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
6. Competition and prey abundance most influential: $\text{group}_{\text{density}} + \text{ungulate}_{\text{winter}} + \text{ungulate}_{\text{summer}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
7. Competition and prey availability most influential: $\text{group}_{\text{density}} + \text{ruggedness} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
8. Prey and mortality risk most influential: $\text{ungulate}_{\text{winter}} + \text{ungulate}_{\text{summer}} + \text{ruggedness} + \text{roads}_{\text{low-use}} + \text{human}_{\text{density}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
9. Competition and mortality risk most influential: $\text{group}_{\text{density}} + \text{roads}_{\text{low-use}} + \text{human}_{\text{density}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$
10. Competition, prey, and mortality risk all influential: $\text{group}_{\text{density}} + \text{ungulate}_{\text{winter}} + \text{ungulate}_{\text{summer}} + \text{ruggedness} + \text{roads}_{\text{low-use}} + \text{harvest}_{\text{density}} + \text{control}_{\text{removals}} + \text{harvest}_{\text{intensity}}$

TABLE A1 Top models for wolf group sizes in Montana, USA, 2005–2018. Variables and their 90% confidence intervals are reported on the log scale and are centered and scaled

Model	Model structure: variable × ß(5% CI, 95% CI)	ΔAIC[a]
Model 7	$B_{intercept}$ × 1.81 (1.735, 1.890) +	0.00
	$group_{density}$ × 0.08 (0.038, 0.122) +	
	ruggedness × −0.05 (−0.085, −0.005) +	
	$harvest_{density}$ × −0.01 (−0.065, 0.035) +	
	$control_{removals}$ × −0.06 (−0.097, −0.027) +	
	$harvest_{restricted}$ × −0.08 (−0.177, 0.008) +	
	$harvest_{liberal}$ × −0.19 (−0.291, −0.083)	
Model 1	$B_{intercept}$ × 1.81 (1.732, 1.888) +	1.46
	$group_{density}$ × 0.07 (0.026, 0.107) +	
	$harvest_{density}$ × −0.01 (−0.064, 0.036) +	
	$control_{removals}$ × −0.06 (−0.094, −0.024) +	
	$harvest_{restricted}$ × −0.08 (−0.173, 0.012) +	
	$harvest_{liberal}$ × −0.18 (−0.286, −0.078)	

[a] Difference in Akaike's Information Criterion from top model.