ARTICLE

Intrinsic and environmental drivers of pairwise cohesion in wild *Canis* social groups

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Abstract

Animals within social groups respond to costs and benefits of sociality by adjusting the proportion of time they spend in close proximity to other individuals in the group (cohesion). Variation in cohesion between individuals, in turn, shapes important group-level processes such as subgroup formation and fission–fusion dynamics. Although critical to animal sociality, a comprehensive understanding of the factors influencing cohesion remains a gap in our knowledge of cooperative behavior in animals. We tracked 574 individuals from six species within the genus *Canis* in 15 countries on four continents with GPS telemetry to estimate the time that pairs of individuals within social groups spent in close proximity and test hypotheses regarding drivers of cohesion. Pairs of social canids (*Canis* spp.) varied widely in the proportion of time they spent together (5%–100%) during seasonal monitoring periods relative to both intrinsic characteristics and environmental conditions. The majority of our data came from three species of wolves (gray wolves, eastern wolves, and red wolves) and coyotes. For these species, cohesion within social groups was greatest between breeding pairs and varied seasonally as the nature of cooperative activities changed relative to annual life history patterns. Across species, wolves were more cohesive than coyotes. For wolves, pairs were less cohesive in larger groups, and when suitable, small prey was present reflecting the constraints of food resources and intragroup competition on social associations. Pair cohesion in wolves declined with increased anthropogenic modification of the landscape and greater climatic variability, underscoring challenges for conserving social top predators in a changing world. We show that pairwise cohesion in social groups varies strongly both within and across *Canis* species, as individuals respond to changing ecological context defined by resources, competition, and anthropogenic disturbance. Our work highlights that cohesion is a highly plastic component of animal sociality that holds significant promise for elucidating ecological and evolutionary mechanisms underlying cooperative behavior.

KEYWORDS

animal sociality, *Canis*, cohesion, cooperative behavior, coyotes, group size, human footprint, wolves

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INTRODUCTION

Understanding sociality and cooperative behavior in animals is a central pursuit of ecology (Alexander, 1974; Clutton-Brock, 2009). Animals should form groups when benefits of close associations with conspecifics, including improved foraging success, group defense, and cooperative breeding, outweigh costs, such as increased competition with group members and greater risk of exposure to disease (Krause & Ruxton, 2002; Silk, 2007). At least two related aspects of sociality influence the costs and benefits of group living to individuals: the size of the group and the amount of time spent with other group members. Ecologists have focused considerable effort investigating causes and consequences of variation in group-size in social animals (e.g., Caraco & Wolf, 1975; Creel & Creel, 1995; Sand et al., 2006; Sells et al., 2022; Vucetich et al., 2004). However, groups are composed of individuals that likely respond to costs and benefits of sociality by adjusting the proportion of time they spend in close proximity to other individuals in the groups (cohesion; Kappeler & van Schaik, 2002). Thus, estimating cohesion between individuals in groups, rather than comparing size across groups, provides a more precise measure of sociality that captures variation in space and time within groups (Wey & Blumstein, 2010). Cohesion has received less research attention than group size despite being a key component of animal social organization and the implicit mechanism by which individuals shape group dynamics that structure animal social systems (Aureli et al., 2008; Kappeler & van Schaik, 2002).

Intrinsic traits of animals are likely to shape their social behavior as individuals can play different functional roles within social groups, often related to cooperative breeding, group foraging, or defensive activities (Cassidy et al., 2017; Josi et al., 2020; MacNulty et al., 2009). For instance, age and breeding status often influence the role and cohesion of individuals within groups (Wey & Blumstein, 2010). Body size could also influence cohesion if larger animals feed on different resources and because defense against other animals is a driver of sociality (Port et al., 2011). Importantly, roles and activities of individuals within groups often vary relative to annual life history patterns and resource availability such that cohesion may change seasonally for social animals (Smith-Aguilar et al., 2016; Wey et al., 2013).

Variation in environmental factors are important drivers of group living in animals (Brown, 1974; Wiszniewski et al., 2009; Wrangham, 1980). Chapman et al. (1995) proposed an ecological constraint hypothesis suggesting that resource competition limits subgroup size and influences fission–fusion dynamics for social animals relative to variation in food availability within and across seasons. Indeed, spotted hyenas (*Crocuta croctua*) were more likely to be with other group members when large, migratory prey were present, suggesting greater cohesion when resources are predictable and abundant (Smith et al., 2008). Gray wolves (*Canis lupus*) feeding on large prey tolerate close proximity with subordinate (usually related) group members because the surplus can be shared and to reduce losses to scavenging (Vucetich et al., 2004). Social foraging and cohesion may also increase for predators when feeding on large prey because of the benefits of coordinated predatory attacks (e.g., Creel & Creel, 1995; MacNulty et al., 2014; Sand et al., 2006). Thus, plasticity in cohesion relative to size and predictability of food should be adaptive and allow animals to adjust sociality relative to temporal variation in resource availability and intragroup competition. Food availability for wild animal populations is difficult to quantify directly across large spatial scales; however, in terrestrial environments, temporal variation in precipitation is negatively correlated with ecosystem productivity, providing a bottom-up index of variation in food resources (Liu et al., 2020; Robinson et al., 2013).

In addition to characteristics of the natural environment, human activity and infrastructure can exert strong influence on animal behavior in time and space. The risk-disturbance hypothesis suggests that human disturbance can act similarly to predation risk and indirectly reduce fitness as animals avoid anthropogenic activity or infrastructure (Frid & Dill, 2002). When considering risk from humans, or predation-risk tradeoffs more generally, an important assumption is that time spent mitigating risk (e.g., through vigilance or avoidance) takes time away from activities such as foraging, parental care, or mating activities (Frid & Dill, 2002; Lima & Dill, 1990). Previous researchers have noted the importance of time as a constraint on sociality and suggested that loss of time resulting from human disturbance could reduce cohesion (Dunbar et al., 2009; Pollard & Blumstein, 2008). Indeed, social animals responding to human disturbance may do so at the cost of adaptive behavior such as exploiting high-quality habitat (Rio-Maior et al., 2019) and engaging in social foraging or grooming (Gall et al., 2022; Marty et al., 2019). Thus, reducing social interactions that increase fitness could result in missed opportunity costs, consistent with predictions of the risk-disturbance and time constraints hypotheses (Frid & Dill, 2002; Gall et al., 2022). Species persecuted by humans are especially likely to adjust behavior in costly ways to avoid disturbance (e.g., Nickel et al., 2021). For instance, groups of chacma baboons (*Papio ursinus*) occupying urban areas altered their movement patterns and exhibited reduced within-group coordination as

individuals mitigated risks associated with humans (Bracken et al., 2022).

Carnivores can play important roles in ecological communities and are declining globally (Fernandez-Sepulveda & Martín, 2022; Ripple et al., 2014), magnifying the value of understanding their social behavior. Canids make an especially effective study group because most canids are social, allowing for comparisons across closely related species with different life-history strategies, morphology, and ecological roles. For instance, wolves are large apex predators, generally rely on large prey, and can be sensitive to human disturbance, whereas coyotes (*Canis latrans*) are medium-sized predators, generalists, and are more resilient to human activities (e.g., Benson et al., 2017). Populations in the genus *Canis* occupy landscapes with a wide diversity of environmental conditions across their geographical distributions from deserts to arctic regions, which may contribute to variation in social behavior relative to biogeographical gradients. Canids in the genus *Canis* form stable, family-based social groups composed primarily of a breeding pair with offspring, although groups sometimes also include unrelated individuals (Mech & Boitani, 2003). Early research on wolves and coyotes with very high frequency (VHF) telemetry established that cohesion was highest for breeding pairs and during winter (Fuller, 1989; Gese et al., 1988; Messier, 1985; Peterson et al., 1984). Wolves in particular are often assumed to be highly cohesive (Mech & Boitani, 2003); however, recent work using global positioning system (GPS) telemetry within single populations suggests that cohesion within these groups can be highly variable (Barber-Meyer & Mech, 2015; Benson & Patterson, 2015; Nordli et al., 2023).

We collected GPS telemetry data from 574 individual canids within the genus *Canis* belonging to social groups from six species (gray wolves, eastern wolves [*Canis lycaon*], red wolves [*Canis rufus*], coyotes, dingoes [*Canis dingo*], and golden jackals [*Canis aureus*], hereafter referred to as canids) in 74 study areas in 15 countries on four continents (Figure 1; Appendix S1: Table S1). We used these data to estimate the proportion of time that pairs within social groups spent in close proximity to investigate drivers of cohesion. Specifically, we tested three non-mutually exclusive hypotheses explaining variation in cohesion linked to costs and benefits of group living. First, we hypothesized that cohesion between pairs within social groups varies as a function of food resource competition relative to prey size, environmental stability, and resource availability (ecological constraints hypothesis; Chapman et al., 1995; Smith et al., 2008). We predicted that wolves are more cohesive than coyotes that generally feed on smaller prey (P1) and that pairwise cohesion in wolves declines with increased availability of suitable small prey (P2). Next, we predicted that cohesion declines with increased variation in precipitation through its negative influence on primary productivity and prey availability (P3). We also predicted that pairwise cohesion should decline in larger groups because of greater within-group competition (P4). Second, we hypothesized that cohesion facilitates group defense to prevent
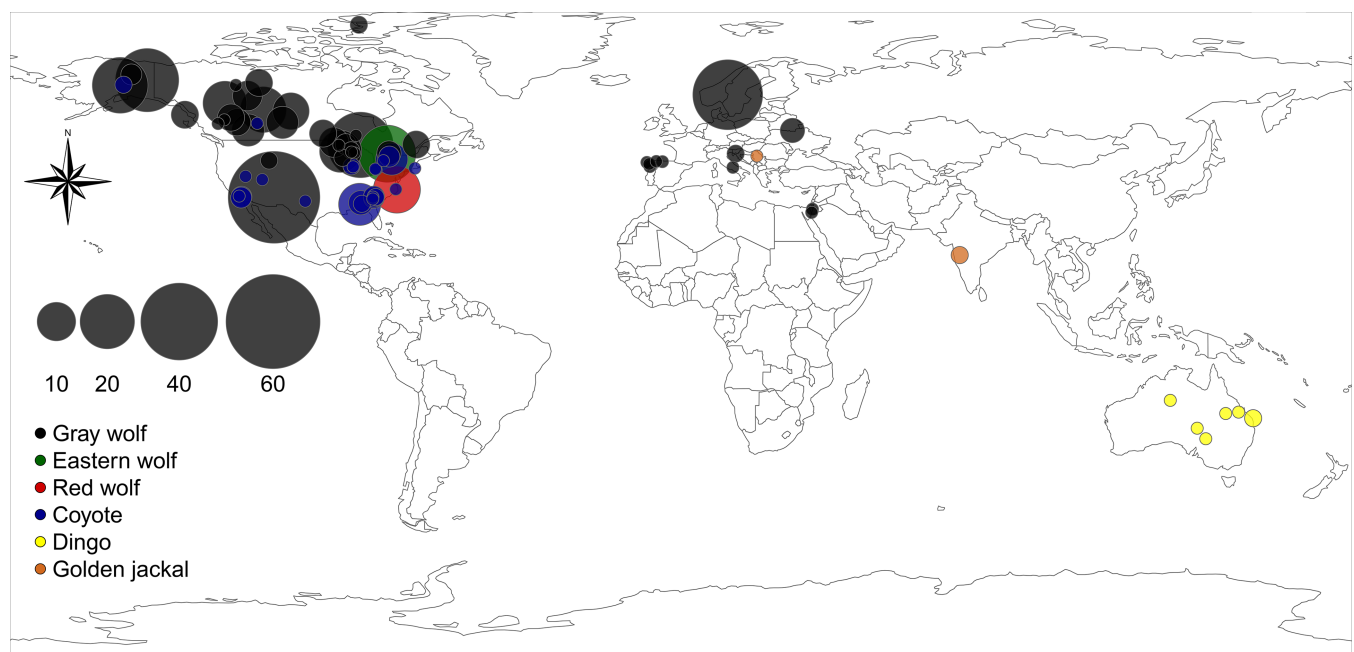

FIGURE 1 Distribution and sample sizes of social pairs of six *Canis* species around the world used to investigate factors influencing cohesion and home range overlap within canid social groups, 2003–2019.

resource loss and mortality (group defense hypothesis; Caraco & Wolf, 1975; Mosser & Packer, 2009) and predicted cohesion to increase when canids are sympatric with other large carnivores (P5). Third, we hypothesized that human disturbance disrupts cohesion within animal social groups, especially those for whom humans pose significant mortality risk, as individuals allocate time to avoiding human activity and infrastructure at the cost of engaging in social interactions (disturbance-time constraints hypothesis; Frid & Dill, 2002; Marty et al., 2019). Here, we predicted that cohesion of canids would decline relative to increased human modification of the landscape (P6). Finally, previous studies have sometimes used home range overlap as a measure of association between animals within social groups (e.g., Albery et al., 2021; Robert et al., 2012). Thus, we also estimated home range overlap between individuals within pairs of social canids with the prediction that cohesion provides a more sensitive measure of association, whereas home range overlap overestimates association (P7). Our work provides a comprehensive evaluation of potential explanations for variation in cohesion of social *Canis* and contributes broadly to understanding cooperative behavior of animals.

METHODS

Study system and field methods

We collected GPS telemetry data from 574 canids within social groups from six species distributed widely across their geographic distributions (Figure 1; Appendix S1: Table S1). The species included gray wolves (*C. lupus*; $n = 408$), eastern wolves (*C. lycaon*; $n = 32$), red wolves (*C. rufus*; $n = 20$), coyotes (*C. latrans*; $n = 89$), dingoes (*C. dingo*; $n = 14$), and golden jackals (*C. aureus*; $n = 6$). Although we refer to the study animals as "canids" throughout, we note that our data and results are restricted to the genus *Canis*. We also included five admixed wolves (*C. lupus* × *C. lycaon*; genetic analyses and treatment of admixture explained in Appendix S2, Section S1: Admixture designation). We programmed GPS collars to collect multiple locations per day (range 2–72). We sexed canids and estimated their ages as pups (0–1), yearlings (1–2), or adults (>2) based on size, tooth characteristics, or from capturing them in natal dens shortly after birth. In many study areas, we took tissue samples for genetic analysis that allowed us to determine breeding status via pedigree analysis (e.g., Benson et al., 2012). In other cases, we determined breeding status by observing evidence of lactation at capture or because a male–female pair were the only adults in a group. For many study animals (70%), we estimated

group size with visual observations, counting tracks, or howling surveys in combination with telemetry. We captured and handled animals in accordance with relevant Institutional Animal Care and Use guidelines and/or government permits (Appendix S1: Table S2).

Estimating cohesion

We estimated the proportion of time that pairs of individuals within social groups spent in close proximity (cohesion) by estimating the Euclidean distance between simultaneous locations (recorded within 5 min) obtained from pairs of canids within social groups. Thus, our use of the term cohesion reflects spatial proximity between individuals within social groups, consistent with previous definitions in the animal social ecology literature (Aureli et al., 2008; Kappeler & van Schaik, 2002). Importantly, our definition of cohesion does not imply understanding the exact nature of interactions between individuals, simply that the individuals were sharing time and space. We considered canids to be in close proximity when simultaneous locations indicated they were within 100 m of each other (Benson & Patterson, 2015). Previous work showed that pairs of canids within social groups spent 91% of their time either <100 m or >1 km from each other, supporting the use of this threshold to estimate cohesion (Benson & Patterson, 2015). Ideally, we would have monitored all animals in every focal pack; however, that was not possible given the difficulty of capturing wild canids and the expense of GPS collars (Benson & Patterson, 2015). We tracked single pairs within many groups, although we did track multiple pairs within a subset of wolf (16% of groups, range 2–29 pairs per group) and coyote (15% of groups, range 2–9 pairs per group) groups. Thus, our strategy was to sample a large number of pairs within social groups across their distributions that captured variation in both intrinsic characteristics (age, breeding status) of individuals and the surrounding environmental conditions. This allowed us to make inference on factors influencing cohesion between pairs in groups, but future research will be needed to understand cohesion of entire groups.

We separated data into three biologically meaningful seasons: den, rendezvous, and winter seasons that are associated with changes in movement, behavior, and important life history events for wolves and coyotes (Harrison et al., 1991; Mech & Boitani, 2003; Oliveira et al., 2020). Breeding females in wolf and coyote groups give birth in dens during spring or early summer where the pups spend most of their first 6–8 weeks (Mech & Boitani, 2003; Oliveira et al., 2020). After leaving the den, wolves and coyotes use pup-rearing (rendezvous) sites

until fall, when the pups either disperse or begin to move with the rest of the pack throughout the winter (Harrison et al., 1991; Mech & Boitani, 2003). We defined den season as the first 8 weeks following the estimated parturition date, rendezvous season as the 16 weeks following den season, and winter as the 28 weeks following rendezvous season. Some GPS collars had variable fix schedules within a given season, so we estimated cohesion using weighted proportions based on the time between sequential locations (locations during shorter intervals were given proportionally less weight) to avoid overrepresenting periods of intensive fixes. We required at least 20 consecutive days of telemetry data within a season to estimate cohesion as the relationship between cohesion and number of monitoring days appeared to stabilize after approximately 20 days (Appendix S2: Figures S1–S3). We estimated seasonal home ranges for each canid to (1) quantify home range overlap between social pairs and (2) generate polygons within which to extract spatial covariates to investigate environmental influences on cohesion. We estimated home range overlap using both adaptive local convex hull and autocorrelated kernel density home range estimators (details in Appendix S2, Section S4: Seasonal home range estimation). Some of the kernel home ranges included large areas that were never visited by study animals, so

we used the overlap estimates from local convex hull home ranges for our main analyses to avoid artificially inflated overlap estimates (see Appendix S2: Figures S4–S8). However, we provide overlap estimates for wolves and coyotes from both the local convex hull and autocorrelated kernel density home ranges for comparison. We inspected all data and excluded data from periods when the canids left the home range such that our estimates of cohesion represent only periods when both canids in a given pair were occupying the territory shared with the group.

Variables influencing cohesion

We estimated multiple variables predicted to influence cohesion for wolves and coyotes to evaluate our hypotheses (Table 1). Given the small numbers of season–pair combinations of dingoes ($n = 10$) and golden jackals ($n = 6$), we excluded them from the multivariate models but included them in descriptive evaluations of cohesion and home range overlap. In the models, we included categorical variables for the four remaining species (gray wolves, eastern wolves, red wolves, and coyotes), three biological seasons, and the three age-classes described above. We also classified each pair as a breeding pair

TABLE 1 Explanatory variables included in generalized additive mixed models used to test three hypotheses and associated predictions (H/P) about drivers of cohesion for pairs of wolves and coyotes in social groups across their distributions, 2003–2019.

Variable	Type	H/P	Models	Description/levels
Species	Categorical, fixed	H1, P1	1	Gray wolf, eastern wolf, red wolf, coyote
Season	Categorical, fixed	...	1–7	Winter, den, rendezvous (Benson & Patterson, 2015)
Age class of pairs	Categorical, fixed	...	1–2, 4, 6	Adult, yearling, pup (Barber-Meyer & Mech, 2015)
Breeding status of pairs	Categorical, fixed	...	3, 5, 7	Breeding, non-breeding (Barber-Meyer & Mech, 2015)
Beavers	Categorical, fixed	H1, P2	2–3, 6	Beavers present or absent in study area
Main prey (wolves)	Categorical, fixed	H1, P2	2–3	Large ungulates or small ungulates/garbage
Main prey (coyotes)	Categorical, fixed	H1, P2	4–5	Ungulates/scavenging or small mammals
Variation in precipitation	Continuous, fixed	H1, P3	2–6	Variation in seasonal precipitation in home range
Pack size	Continuous, fixed	H1, P4	6–7	No. canids in social group
Large predators	Categorical, fixed	H2, P5	2–5	Mountain lions, bears, wolves
Region	Categorical, fixed	...	4–5	Western coyotes, eastern coyotes
Landscape alteration	Continuous, fixed	H3, P6	2–7	Anthropogenic landscape alteration in home range
Human-caused mortality	Categorical, fixed	...	2–5	Exploitation by humans heavy or light/nonexistent
Pair	Categorical, random	...	1–7	Animals in pair
Pack	Categorical, random	...	1–7	Social group
Study area	Categorical, random	...	1–7	Local region where research was conducted

Note: H1 is the ecological constraints hypothesis, H2 is the resource defense hypothesis, and H3 is the disturbance-time constraints hypothesis. Also shown are models that included each variable, where Model 1 included both wolves and coyotes, Models 2–3 and 6 included only wolves, and Models 4–5 and 7 included only coyotes.

(male and female breeders) or non-breeding pair (any pair with one or more nonbreeders). Although not central to our hypotheses and predictions, we explored potential differences in cohesion between different sex combinations within pairs in preliminary models for wolves and coyotes. These models indicated that different sex combinations did not strongly influence cohesion (results shown in Appendix S3: Tables S1 and S2), so we did not consider the influence of sex further to reduce model complexity.

To evaluate support for the ecological constraints hypothesis, we compared cohesion of wolves and coyotes to test the prediction that wolves relying on large prey (Benson et al., 2017; Carbone et al., 1999) are more cohesive than coyotes (P1). We also created a binary variable for each pair depending on whether beavers (Castor canadensis or Castor fiber) were present in study areas occupied by wolves. Wolves kill a variety of other small non-ungulate prey such as hares (Lepus spp.) and salmon (Oncorhyncus spp.) across their range; however, predation on such prey is generally opportunistic or consistent only in specific regions (Gable et al., 2018). Conversely, beavers are important prey for wolves in most areas where the two species are sympatric across large portions of North America, Europe, and Asia, comprising 5%–60% of their estimated annual or seasonal diets (Gable et al., 2018; Peterson & Ciucci, 2003). Thus, we predicted that wolves would be less cohesive when this important small prey was available (P2). We also created a categorical variable for the dominant prey in the diet of canids within each study area (P2; Table 1; Appendix S2: Section S5: Additional details of predictor variables). In some cases, this was based upon previous research, but when such information was not available, this variable was based upon the opinion of researchers working in the area. Coyotes in eastern North America are larger and appear to prey on ungulate prey more than western coyotes, which may be due to historical or contemporary hybridization with wolves (Benson et al., 2012). Thus, we included a variable that separated coyotes from eastern and western North America to evaluate whether cohesion of coyotes differed by region (additional details in Appendix S2, Section S5: Additional details of predictor variables). Additionally, we included a variable for the coefficient of variation in precipitation within seasonal monitoring periods with the prediction that cohesion would be reduced with increased variability (P3). We had group size information for many of the canid pairs (70% of wolves, 71% of coyotes), so we created subset models with these data with the prediction that cohesion would be lower in larger groups (P4). To evaluate the group defense hypothesis, we created a binary variable for the presence of larger predators (mountain lions [Puma concolor], black bears [Ursus americanus], brown bears [Ursus arctos], polar bears [Ursus maritimus], or wolves [for coyotes]) within the different study areas (P5). To evaluate the disturbance-time constraints hypothesis, we included a spatial variable for the proportion, intensity, and type of anthropogenic modification of the landscape within each home range using the global human modification dataset (P6; Kennedy et al., 2019). This dataset provides an empirically based, continuous variable of the proportion of the landscape that is modified by humans (0–1) at a 1-km^2 resolution. These data represent estimates of modification from 13 anthropogenic stressors organized within five major categories (human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure; Kennedy et al., 2019). Finally, we included a binary variable indicating whether human-caused killing of wolves and coyotes was heavy or light/absent based upon observations of researchers working in each study area. This variable allowed us to consider whether variation in human-caused exploitation influenced cohesion. Additional details of predictor variables are available in Table 1 and Appendix S2, Section S5: Additional details of predictor variables.

Analysis and modeling

We modeled the relationship between cohesion (response variable) and intrinsic and environmental variables predicted to influence cohesion (Table 1) using generalized additive mixed models (GAMMs) estimated using restricted maximum likelihood (Wood, 2006). We transformed the proportional response variable using the logit transformation to meet the assumptions of regression (Warton & Hui, 2011). We included categorical variables as fixed, parametric effects and continuous variables as fixed, nonparametric smooth terms (thin-plate regression splines). The smooth terms fit within GAMMs allowed us to identify potential nonlinear relationships between continuous predictor variables and cohesion, whereas if nonlinearity was not supported these relationships defaulted to linear effects (Wood, 2006). Along with the smooth term for anthropogenic landscape modification, we included a "by" term for the factor variable of season to investigate whether there were different relationships between human disturbance and cohesion during the winter and pup-rearing seasons. The "by" term estimates a separate smooth function to model relationships between the continuous variable (in this case human-landscape alteration) and each level of the factor variable (season), which is functionally similar to fitting an interaction term (Wood, 2006). We

included a random intercept for pair nested in pack nested in study area to account for the lack of independence of cohesion data from the same pair, pack, and study area. We also included a smooth, fixed interaction term with spatial coordinates for the centroid of the shared home range for each pair to account for spatial autocorrelation (Beale et al., 2010). None of our predictor variables were highly correlated (all |r| < 0.53). We did not use an information criterion approach for model selection, which can be unreliable with GAMMs (Wood & Augustin, 2002). Instead, we included all variables predicted to influence cohesion (Table 1) in global models and adopted a simple procedure for retaining variables recommended for generalized additive models by Wood and Augustin (2002), modified for use with GAMMs. Specifically, we removed less informative predictor variables ($p > 0.20$), sequentially, beginning with the least influential variable and then reran the simpler models until we identified a parsimonious model.

We began by investigating differences in cohesion between wolves and coyotes, while also accounting for season and age (Model 1, wolves and coyotes; Table 1). Then, we progressed to wolf- and coyote-specific models to investigate factors hypothesized to influence cohesion within wolves and coyotes separately to avoid overly complex models with multiple interactions given that we expected differences in cohesion between wolves and coyotes. Specifically, we created global models with variables for either (1) age class (Model 2, wolves; Model 4, coyotes) or (2) breeding status (Model 3, wolves; Model 5, coyotes) along with the other predictor variables for wolves and coyotes (Table 1). We did not include age class and breeding status in the same models to avoid redundancy as all breeders were adults. Evaluating models with age class, in addition to those with breeding status, allowed us to include a larger sample of pairs in these models because we did not know the breeding status of all individuals. Additionally, understanding whether adults can be used as a reasonable proxy for breeders in studies of wolf and coyote sociality may be useful to future studies that do not have information regarding breeding status. Finally, we modeled cohesion with the variables retained in the most strongly supported models for wolves and coyotes with the subset of data for which we had pack size estimates (Model 6, wolves; Model 7, coyotes) to test the prediction that cohesion decreases in larger groups (P4; Table 1). We also created two simple models to evaluate potential differences in home range overlap between wolves and coyotes, while accounting for potential differences across seasons and between breeding pairs (relative to pairs with nonbreeders; Model 8) or adult pairs (relative to pairs with younger animals, Model 9). For parametric terms, we show beta coefficients and 95%

confidence intervals (CIs). For nonparametric smooth terms, we show estimated degrees of freedom (edf) and estimated p-values. We provide adjusted R^2 values as estimates of the variation explained. We conducted modeling with the "gamm4" package (v. 0.2-6) in R (v. 4.1.2).

RESULTS

Patterns of cohesion and home range overlap

Pairs of canids within social groups exhibited wide variation in cohesion ranging from 5% to 100% during seasonal monitoring periods. There was considerable variation in pair cohesion across different species of canids (Figure 2a). Gray wolves ($n = 641$ seasonal pairs, 408 individuals) and eastern wolves ($n = 29$ seasonal pairs, 32 individuals) were more cohesive than coyotes ($n = 125$ seasonal pairs, 89 individuals; Figure 2a). The point estimate for cohesion of red wolves ($n = 36$ seasonal pairs, 20 individuals) was lower than other wolf species (Figure 2a), although this difference was not evident once we accounted for other factors influencing cohesion in multivariate models (see below). Point estimates for dingoes ($n = 10$ seasonal pairs, 14 individuals) were similar to coyotes in cohesion, whereas estimates for golden jackals ($n = 6$ seasonal pairs, six individuals) were higher (Figure 2a). However, samples sizes were small for dingoes and golden jackals such that we could not statistically evaluate their cohesion relative to other *Canis* species. Home range overlap between social pairs was more consistent among the different species of canids relative to the wider variation in cohesion (Figure 2). Mean home range overlap ranged from 0.58 in dingoes (SD = 0.12, $n = 10$ seasonal pairs) to 0.76 in golden jackals (SD = 0.17, $n = 6$ seasonal pairs; Figure 2b).

Coyotes were less cohesive than all wolves combined ($\beta = -0.42$, 95% CI [−0.60, −0.26]; Model 1, Figure 3). Wolves and coyotes were both more cohesive during winter than in den and rendezvous seasons ($\beta = 0.43$, 95% CI [0.36, 0.50]; Model 1, Figure 3; Appendix S4: Table S1), whereas cohesion did not differ between den and rendezvous seasons ($\beta = 0.02$, 95% CI [−0.05, 0.10]). Thus, for the remaining analyses, we combined den and rendezvous seasons.

Factors influencing cohesion of wolves

The most parsimonious models for wolf cohesion with age class ($R^2 = 0.31$, $n = 666$ seasonal pairs; Model 2, Table 2) or breeding status ($R^2 = 0.32$, $n = 543$ seasonal pairs; Model 4; Appendix S4: Table S2) produced similar
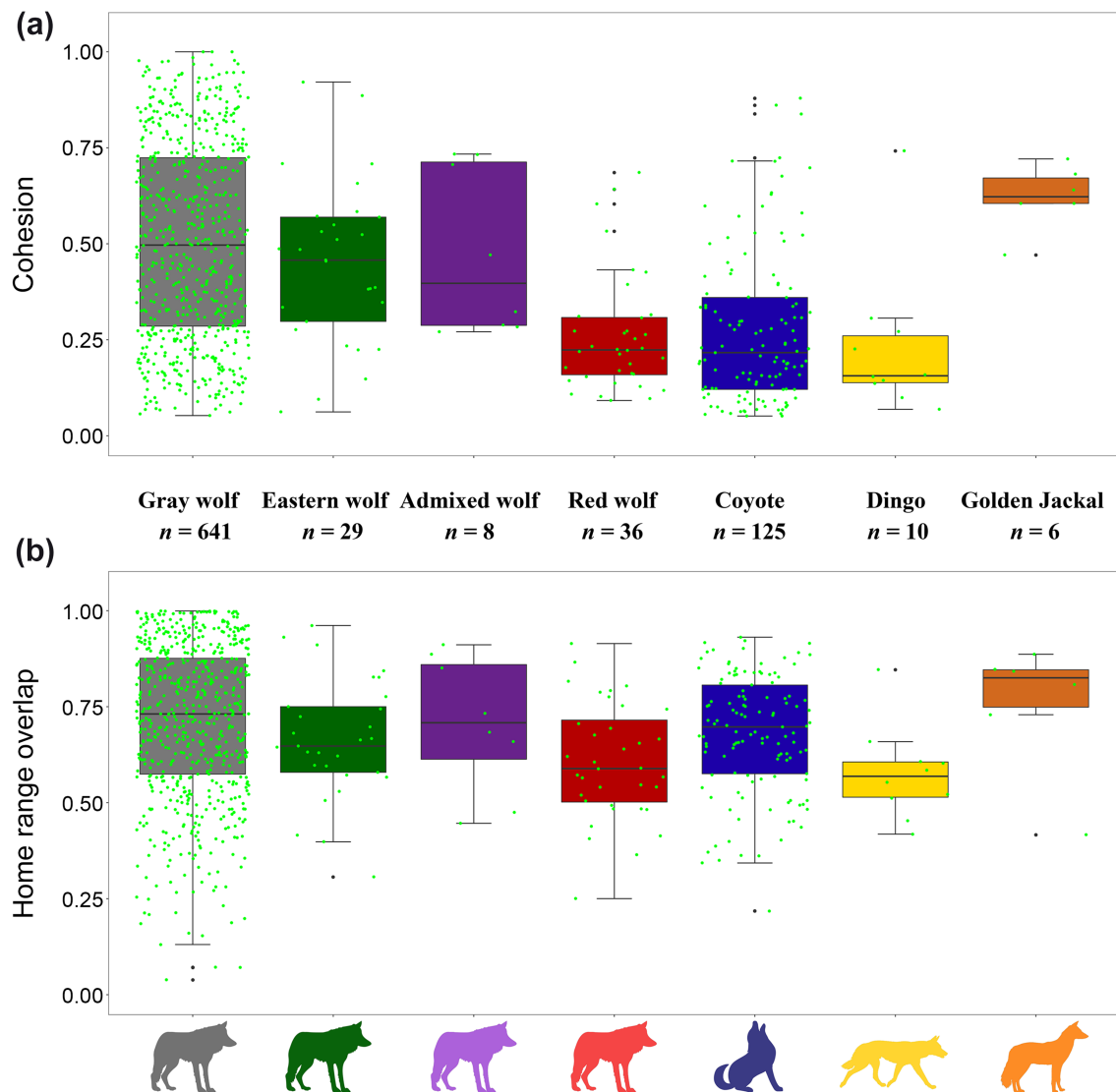
F I G U R E 2 Boxplots showing (a) cohesion and (b) home range overlap between social pairs of canids, 2003–2019, estimated from telemetry data. Black lines in boxes are median values, boxes are bounded by the 25th and 75th percentiles (interquartile range), error bars include the largest values within 1.5 × the interquartile range, black circles are values outside of 1.5 × the interquartile range, and green circles are all data values. Sample sizes are season–pair combinations.

parameter estimates and model fit. Adult pairs were more cohesive than pairs with younger wolves ($\beta = 0.23$, 95% CI [0.13, 0.32]; Model 2). Breeding pairs ($\bar{x}_{\text{winter}} = 0.72$, SD = 0.23, $n = 49$, $\bar{x}_{\text{pup-rearing}} = 0.46$, SD = 0.21, $n = 51$) were more cohesive than pairs involving nonbreeders ($\bar{x}_{\text{winter}} = 0.54$, SD = 0.25, $n = 253$, $\bar{x}_{\text{pup-rearing}} = 0.39$, SD = 0.21, $n = 190$; Appendix S5: Table S1; $\beta = 0.37$, 95% CI [0.23, 0.50]; Model 4; Figure 3; Appendix S4: Table S2). We tested the remaining predictions using the model with age class (Model 2) to take advantage of the larger sample size, but full results from the model with breeding status were consistent (Appendix S4: Table S2). The model with age class indicated that cohesion of wolves was higher in winter ($\beta = 0.46$, 95% CI [0.40,

0.52]) and lower in the presence of beavers ($\beta = -0.30$, 95% CI [−0.57, −0.02]). Variation in precipitation negatively influenced wolf cohesion (edf = 2.5, $p = 0.004$). Data from Israel included extreme values for variation in precipitation relative to the rest of the dataset, but results were similar without data from Israel (Appendix S6: Table S1). Variation in precipitation also had a consistent influence on cohesion in the subset model with group size (see below) that did not include data from Israel (edf = 1.0, $F = 10.8$, $p = 0.001$; Figure 4a; Table 2, Model 6). Human modification to the landscape negatively influenced cohesion of wolves in winter (edf = 3.2, $p < 0.001$), but not in pup-rearing seasons (edf = 1.0, $p = 0.888$; Figure 4b). In winter, cohesion declined sharply in landscapes ranging
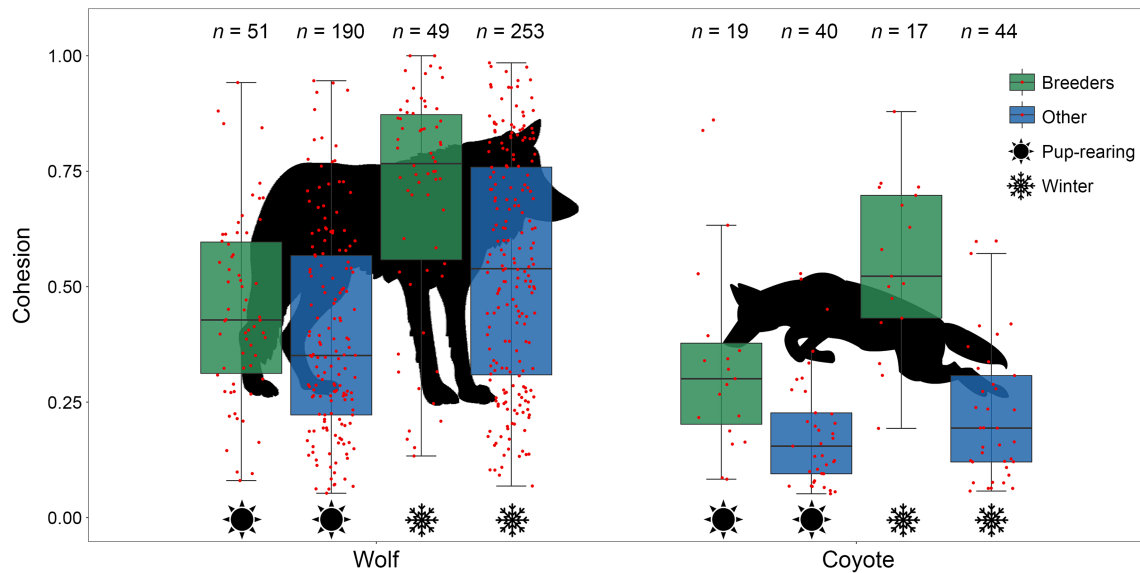
FIGURE 3 Cohesion of social pairs of wolves and coyotes during winter and pup-rearing. Pairs are separated as breeding pairs and pairs containing at least one nonbreeder (other pairs). Black lines in boxes are median values, boxes are bounded by the interquartile range, error bars include the largest values within 1.5× the interquartile range, and red circles are all data values. Sample sizes are season-pair combinations.

TABLE 2 Results from parsimonious overall (Model 2) and subset (Model 6; with inclusion of pack size) generalized additive mixed models used to investigate intrinsic and extrinsic factors influencing time spent in close proximity (<100 m) by social pairs of wolves across their geographic distribution, 2003–2019.

Variable	Overall model ($n = 666$)		Model with pack size ($n = 451$)	
Parametric terms	**β**	**95% CI**	**β**	**95% CI**
Adult pair[a]	0.23	(0.14, 0.32)	0.18	(0.08, 0.28)
Winter[b]	0.46	(0.40, 0.52)	0.49	(0.43, 0.55)
Beavers present[c]	−0.30	(−0.57, −0.02)	−0.36	(−0.61, −0.11)
Smooth terms	**edf**	**p**	**edf**	**p**
Human landscape alteration (pup-rearing)	1	0.888	1	0.717
Human landscape alteration (winter)	3.2	<0.001	3.1	<0.001
Variation in precipitation	2.5	0.004	1	0.001
Pack size	...	...	2.1	0.004
Latitude × longitude	3.1	0.110	5	0.001

Note: We show β coefficients and 95% CIs for parametric effects and estimated df (edf) and *p* values for smooth terms. All parametric terms were categorical.
[a]Reference is pairs with ≥1 pup or yearling.
[b]Reference is pup-rearing seasons (den and rendezvous).
[c]Reference is no beavers present.

from minimal to moderate landscape alteration before the relationship plateaued at higher levels of landscape modification (Figure 4b). Eastern (β = 0.06, 95% CI [−0.31, 0.44]) and red (β = 0.03, 95% CI [−0.57, 0.62]) wolves did not differ in cohesion from gray wolves. Cohesion did not differ for pairs in areas with higher wolf exploitation from those with no or low wolf exploitation (β = −0.02, 95% CI [−0.20, 0.17]). Cohesion did not differ in the presence of other species of large predators (β = −0.09, 95% CI [−0.35, 0.18]) or for wolves whose primary prey was believed to be large ungulates (β = 0.08, 95% CI [−0.07, 0.23]). Including a variable for group size reduced sample size, but increased explanatory power ($R^2 = 0.48$, $n = 451$ seasonal pairs; Model 6, Table 2), indicating that wolf pairs were
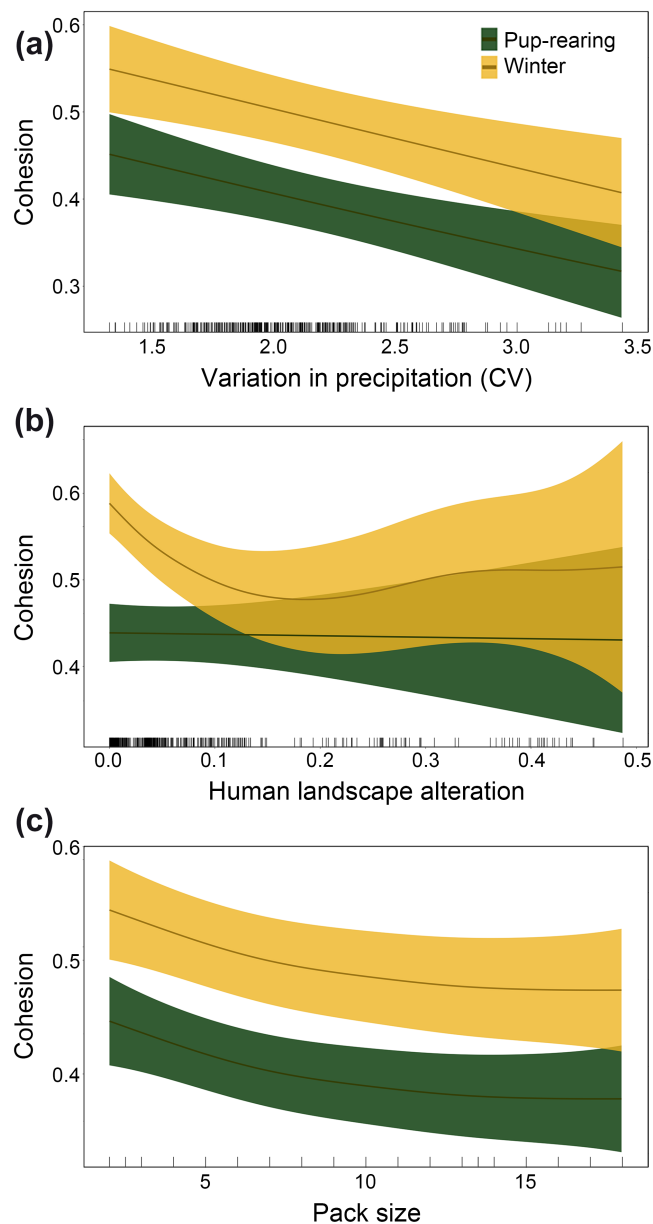
FIGURE 4 Relationships between cohesion of social wolf pairs and (a) variation in precipitation (CV), (b) anthropogenic landscape modification, and (c) group size across their geographic distribution in winter and pup-rearing seasons as estimated with generalized additive mixed models.

less cohesive as group size increased (supporting P4; edf = 2.1, $p = 0.004$; Figure 4c).

Factors influencing cohesion of coyotes

The most parsimonious models for coyote cohesion from model sets with age class ($R^2 = 0.15$, $n = 125$ seasonal pairs; Model 4) or breeding status ($R^2 = 0.42$, $n = 120$ seasonal pairs; Model 5) retained the same variables, but the model with breeding status explained almost 3 times the variation in cohesion (Appendix S4: Tables S3 and S4). Thus, we made inference on the model with breeding status. Cohesion was greater for breeding coyote pairs ($\bar{x}_{\text{winter}} = 0.55$, SD = 0.18, $n = 17$, $\bar{x}_{\text{pup-rearing}} = 0.35$, SD = 0.22, $n = 19$) compared with pairs containing nonbreeders ($\bar{x}_{\text{winter}} = 0.21$, SD = 0.15, $n = 44$, $\bar{x}_{\text{pup-rearing}} = 0.18$, SD = 0.12, $n = 40$; $\beta = 0.51$, 95% CI [0.33, 0.70]; Figure 3; Appendix S5: Table S1). Cohesion was also greater for coyotes in winter than in pup-rearing seasons ($\beta = 0.19$, 95% CI [0.11, 0.28]; Model 5, Figure 3). Human modification to the landscape exhibited a negative relationship with cohesion of coyote pairs that approached significance (edf = 2.1, $p = 0.088$). Cohesion did not differ between western and eastern coyotes ($\beta = -0.05$, 95% CI [−0.84, 0.74]). Cohesion did not differ between pairs in areas with no or low coyote exploitation and those with higher coyote exploitation ($\beta = 0.24$, 95% CI [−0.21, 0.69]). Cohesion was not different in the presence of large predators ($\beta = -0.15$, 95% CI [−0.52, 0.23]) or for coyotes whose main prey was believed to be ungulates ($\beta = -0.11$, 95% CI [−0.35, 0.13]). Cohesion of coyotes was not influenced by variation in precipitation (edf = 2.6, $p = 0.239$). With the inclusion of group size, the amount of variation explained by the model increased despite the reduction in sample size ($R^2 = 0.53$, $n = 81$ seasonal pairs; Model 7). There was a negative trend in pairwise cohesion in larger coyote groups, but the CIs for this effect overlapped zero ($\beta = -0.36$, 95% CI [−0.79, 0.08]).

Factors influencing home range overlap

Models evaluating factors influencing home range overlap of wolves and coyotes provided similar results with breeding status ($R^2 = 0.15$, $n = 663$ seasonal pairs; Model 8) or age class ($R^2 = 0.15$, $n = 791$ seasonal pairs; Model 9; Appendix S7: Table S1). Home range overlap was greater for breeding pairs relative to pairs involving nonbreeders ($\beta = 0.26$, 95% CI [0.15, 0.38]; Model 8) and for adult pairs relative to pairs involving younger animals ($\beta = 0.20$, 95% CI [0.11, 0.30]; Model 9). Home range overlap was greater during winter than pup-rearing seasons (Model 8: $\beta = 0.41$, 95% CI [0.34, 0.48]; Model 9: $\beta = 0.47$, 95% CI [0.40, 0.54]). However, home range overlap did not differ between wolves and coyotes (Model 8: $\beta = -0.13$, 95% CI [−0.29, 0.02]; Model 9: $\beta = -0.07$, 95% CI [−0.22, 0.08]). Mean home range overlap by season, breeding status, and age class for wolves and coyotes from both adaptive local convex hull and autocorrelated kernel home range estimates are provided in Appendix S5: Table S2.

DISCUSSION

Individuals in *Canis* social groups repeatedly engaged and disengaged in context-specific pairwise associations resulting in wide variation in cohesion (5%–100%) in time and space. Our models indicated that cohesion varied strongly relative to intrinsic characteristics of individuals within groups (species, age, breeding status), as well as changing ecological and anthropogenic context defined by resources, competition, and landscape alteration. Our results support the ecological constraints hypothesis that animal sociality is limited by factors that influence the strength of competition within groups (Chapman et al., 1995). Prey size influenced cohesion both across and within species, as wolves were more cohesive than coyotes (P1) and cohesion declined for wolves in the presence of suitable small prey (beavers; P2). Although coyotes can kill large prey and are effective deer predators in some areas, their relatively small body mass frees them from relying on large prey (Carbone et al., 1999) such that their diet is often dominated by small prey supplemented with vegetation and anthropogenic food (Benson et al., 2017; Jensen et al., 2022). Coyotes in eastern North America are larger and appear to prey on ungulates more than western coyotes (e.g., Benson & Patterson, 2013; Jensen et al., 2022), which may be due to historical or contemporary hybridization with wolves (Benson et al., 2012). However, even in eastern North America, coyotes often prey on small prey and anthropogenic food more than wolves (Benson et al., 2017). Smaller food patches or items increase competition within animal social groups (Wrangham, 1980), which favors lower cohesion that may allow coyotes to partition resources within territories shared by family groups. Indeed, feeding on small mammals may be a mechanism by which coyote pups reduce competition with adults in coyote packs (Gese et al., 1996). Conversely, feeding on large prey reduces competition within groups of wolves by providing a surplus of food that can be shared with relatives, rather than being lost to scavengers, favoring delayed dispersal and cohesion that provides inclusive fitness benefits (Mech & Boitani, 2003; Vucetich et al., 2004).

When small prey in the form of beavers was available, wolves were less cohesive, further highlighting ecological constraints on sociality. As noted above, beavers are the most consistent non-ungulate prey used by wolves across large portions of their geographic range (Gable et al., 2018). Lower cohesion in the presence of beavers is consistent with previous reports that a single wolf can consume an entire beaver in less than an hour (Gable et al., 2016; Peterson & Ciucci, 2003). We found no difference in cohesion between wolves feeding primarily on large or small ungulates, or for coyotes primarily feeding on larger prey, but acknowledge that most of our data on primary prey types were observational. Regardless, our results with respect to beavers suggest wolves adjust cohesion relative to prey size and corresponding changes in intragroup competition that favor greater or lesser cohesion with larger and smaller prey, respectively. Similarly, spotted hyenas formed larger subgroups when large prey was available and quickly congregated at kills (Smith et al., 2008). Associations within subgroups of African lion (*Panthera leo*) prides weakened when large prey were available, but individuals associated more evenly with all members of the pride when exploiting large prey (Mbizah et al., 2020).

Pairwise cohesion in wolf groups also declined with increasing variation in precipitation (consistent with P3), further supporting the ecological constraints hypothesis. Seasonal variation in precipitation is a strong predictor of ecosystem productivity (Robinson et al., 2013) such that our results suggest cohesion is highest for wolves in stable, productive environments where competition for food is reduced (Brown, 1974; Chapman et al., 1995). Spotted hyenas and African lions are also more gregarious when prey is abundant and competition is relaxed (Mbizah et al., 2020; Smith et al., 2008). Thus, plasticity in cohesion relative to variable climatic conditions appears to allow large, social carnivores to adjust their cooperative behavior in response to changing benefits (e.g., surplus at kills) and costs (e.g., intragroup competition when prey is scarce or small) of sociality when resources are unpredictable within seasons. Wolves in our study also exhibited reduced cohesion with increasing group size (consistent with P4), as shown previously for wolves attending prey carcasses in Yellowstone National Park (Metz et al., 2011). Formation and reduced size of subgroups within larger animal groups are also driven by limited food availability and higher intragroup competition, as shown in primates and elephants (Chapman et al., 1995; Wittemyer et al., 2005). Changes in pairwise cohesion and formation of subgroups are related outcomes of fission–fusion dynamics that both appear to be driven by variation in resources and corresponding changes in competition within larger groups.

We found no support for the group defense hypothesis as cohesion did not increase in the presence of other large carnivore species (P5). Even for canid pairs exhibiting low cohesion, time spent with groupmates likely peaks when feeding on large prey carcasses (Metz et al., 2011), which is also when interactions with bears and other large carnivores are most likely to occur (Ordiz et al., 2015). Thus, context-specific cohesion at feeding sites may provide sufficient defense against other species of scavenging large carnivores. Perhaps more

importantly, intraspecific strife is often the leading cause of natural mortality in wolf populations (Cubaynes et al., 2014) such that defense against conspecifics may be a more important driver of sociality. Unfortunately, we did not have reliable estimates of local canid density across our study areas, which would be an important variable to consider with future research. For coyotes, group size can influence the outcome of interactions with wolves. In Yellowstone National Park, wolves represent significant mortality risk for coyotes and generally dominate interactions with the smaller canids; however, when coyotes outnumbered wolves, they harassed, chased, or even attacked wolves (Merkle et al., 2009). Following the reintroduction of wolves to Yellowstone, coyote density and group size declined, whereas cohesion within coyote packs increased (Crabtree & Sheldon, 1999). This is consistent with our finding of greater cohesion in smaller packs, but inconsistent with our failure to detect differences in cohesion relative to the presence of sympatric large carnivores.

Pairwise cohesion in wolves, and to a lesser degree coyotes, declined with greater human landscape alteration during winter (consistent with P6), the season when they are normally most cohesive. This supports the hypothesis that avoiding disturbance disrupts social cohesion of animals occupying landscapes altered by humans. California ground squirrels (*Otospermophilus beecheyi*) reduced greeting behaviors, sitting in close proximity, and social foraging following disturbances by humans, resulting in lower cohesion and potential missed opportunity costs (Gall et al., 2022). Long-tailed macaques (*Macaca fascicularis*) spent more time monitoring humans visually at the cost of time spent grooming their social partners, suggesting that human disturbance imposes time constraints on social interactions (Marty et al., 2019). Cohesion of wild wolves may be constrained in an analogous fashion if their avoidance of human infrastructure and activity (Lesmerises et al., 2012; Rio-Maior et al., 2019) disrupts social activities. Large carnivores often exhibit circuitous travel paths as they avoid human activity and infrastructure in fragmented landscapes (Benson et al., 2021; Nickel et al., 2021), which could delay reunions between individual wolves and reduce cohesion. The loss of breeding animals to mortality can lead to dissolution of social groups for wolves (Brainerd et al., 2008), highlighting a direct mechanism by which humans disrupt animal social structure (but see Goldenberg et al., 2016). However, we did not detect variation in cohesion for pairs of wolves or coyotes across areas with higher and lower human-caused mortality. Rather, our results suggest that humans may influence sociality of wolves indirectly, as inefficient movement or other time constraints resulting from

avoiding human disturbance may have reduced time allocated to cooperative activities related to foraging, breeding, or defense.

Consistent with previous findings within single populations, we found that breeding pairs were the most cohesive individuals within canid groups and that wolves and coyotes were more cohesive during winter than during pup-rearing seasons (Barber-Meyer & Mech, 2015; Bekoff & Wells, 1980; Benson & Patterson, 2015; Gese et al., 1988; Nordli et al., 2023; Peterson et al., 1984). This reflects that the breeding animals are the core of family-based wolf and coyote groups. Canid groups abandon pup-rearing sites in autumn and are thought to travel together throughout winter (Mech & Boitani, 2003). Cohesion between breeding pairs increases during the winter mating season, but then declines considerably during pup-rearing in spring and summer (Gese et al., 1988; Nordli et al., 2023; Patterson & Messier, 2001). Reduced cohesion during pup-rearing is partially related to different contributions by group members to cooperative breeding, as breeding females attend to pups in dens, whereas breeding males provision females and pups (Mech & Boitani, 2003; Rio-Maior et al., 2018). Thus, in addition to testing new hypotheses about drivers of cohesion, our work across much of the range of wolves and coyotes corroborates understanding of their social behavior relative to annual life history patterns derived from decades of population-level studies. We also show that home range overlap provides a less variable, spatially and temporally coarse index of sociality that appears to overestimate degree of association between individuals relative to telemetry-based estimates of cohesion (consistent with P7). Home range overlap estimates were higher with the autocorrelated kernel density estimator than with adaptive local convex hulls, but both home range overlap estimators provided greater and less variable estimates of association between pairs of social wolves and coyotes than the corresponding cohesion estimates (supporting P7; Appendix S5: Tables S1 and S2). However, GPS telemetry provides an effective tool for quantifying social association via cohesion for elusive species directly with high spatial and temporal resolution.

As noted above, an important limitation of our data is that we sampled pairs within groups to measure cohesion, rather than monitoring entire groups. GPS tracking of all individuals within wild canid social groups is rarely feasible, especially at the scale of our current study. Indeed, most canid researchers attempt to maximize sampling across, rather than within packs, which has limited understanding of social dynamics (Benson & Patterson, 2015). To begin to address this knowledge gap, we sampled pairs within groups across large portions of

the geographic ranges of wolves and coyotes to capture variation in intrinsic and environmental factors influencing cohesion. This provided inference on pairwise cohesion that allowed us to provide new insight on factors influencing intragroup associations of wolves and coyotes. Future studies that are able to monitor all (or higher proportions of) individuals within canid groups, even in small areas with limited numbers of packs, would contribute important additional understanding regarding cohesion in canid social groups. We also acknowledge that there is important behavioral nuance in the interactions of canids within social groups that is only possible to detect with direct observation (e.g., Baan et al., 2014; Gese, 2001). Another limitation of our data is that we were unable to sample cohesion of golden jackals and dingoes sufficiently for comprehensive inference. The dingoes in our dataset exhibited relatively low cohesion, similar to coyotes, consistent with previous reports (Thomson, 1992). Interestingly, golden jackals appeared to exhibit high cohesion, more similar to that of wolves.

Beyond the genus *Canis*, a recent study suggested that food sharing strategies within African wild dog groups (*Lycaon pictus*) may influence carcass attendance (and thus cohesion; Jordan et al., 2022). Studies of several species of foxes (*Vulpes* spp.) have investigated sociality by estimating cohesion, home range overlap, or the proportion of locations indicating pairs were sharing dens using VHF telemetry (e.g., Doncaster & Macdonald, 1997; Kamler & Macdonald, 2014; Kitchen et al., 2005; Ralls et al., 2007). These studies suggest similarities and differences between cohesion of fox pairs with that of wolves and coyotes. For instance, swift foxes were closer together during winter (breeding) than during spring and summer (pup-rearing) similar to our findings (Kitchen et al., 2005). Breeding pairs of red foxes (*Vulpes vulpes*) were located in close proximity during 11%–33% of nightly activity bouts (Doncaster & Macdonald, 1997), which suggests lower cohesion than the breeding wolves and coyotes in our study (Figure 3). However, we are unaware of previous studies estimating cohesion of fox pairs more continuously and accurately with GPS telemetry or evaluating intrinsic and extrinsic factors influencing cohesion of foxes. This should now be possible as smaller GPS collars suitable for foxes have recently become available (e.g., Walton et al., 2018). Future studies using GPS telemetry to evaluate cohesion with wider taxonomic and geographic scope will add greatly to our understanding of both canid and animal sociality.

Individual animals can make permanent changes to their social environment by leaving or excluding others from the group (Bekoff, 1977; Nordli et al., 2023). Alternatively, individuals can retain the benefits of group living, while minimizing costs, by adjusting cohesion through time relative to variation in their physiological or behavioral state, as well as the surrounding environmental conditions. Animal societies with fission–fusion dynamics were traditionally considered rare among mammals (reviewed by Aureli et al., 2008). Aureli et al. (2008) pointed out that classifying animal social structure as binary alternatives (e.g., "cohesive" or "fission–fusion") is a false dichotomy and that fission–fusion dynamics occur to varying degrees in most animal social systems. Indeed, canids in the genus *Canis* form stable, highly cooperative social groups (Mech & Boitani, 2003); yet our results highlight that they exhibit fission–fusion dynamics as individuals vary in pairwise cohesion relative to their roles within groups and the surrounding environmental conditions. Our work also supports broad theoretical predictions that food abundance and quality modulate social group dynamics (Giraldeau & Caraco, 2000; Stephens & Krebs, 1986). We contribute to growing evidence that various aspects of sociality, including group size, subgroup dynamics, and cohesion, vary relative to changes in resource conditions and intragroup competition for a variety of mammalian taxa (Chapman et al., 1995; Lehmann et al., 2007; Lusseau & Newman, 2004; Mbizah et al., 2020; Smith et al., 2008; Wittemyer et al., 2005).

Changes in pairwise cohesion of wolves with increased variation in climate and the expanding global human footprint may have broad implications for future population dynamics and ecological function of these highly interactive predators. Climate-change assessments project increasing variation in precipitation associated with warming temperatures and greater frequency of extreme rainfall and drought events (e.g., IPCC, 2021; Zhang et al., 2021), while anthropogenic modification of landscapes continues around the world (Kennedy et al., 2019). For instance, the North American Boreal Forest biome, across which wolves are ubiquitous and much of our data were collected, is under increasing pressure from proposed infrastructure development projects involving large-scale mining, oil and gas extraction, timber harvest, hydropower, and other industrial activities within remote roadless areas (Wells et al., 2020). Recently, some ecologists have suggested that social animals might be well-suited to meet the challenge of rapid environmental changes that exceed the pace of genetic adaptation because of increased phenotypic plasticity of species that form groups and cooperate in tasks that influence fitness (Komdeur & Ma, 2021; Taborsky et al., 2021). Our documentation of plasticity in cohesion by canids may support this contention. However, reduced social cohesion relative to climate variability and increasing human footprint might also be cause for concern given the importance of sociality to predation, population

growth, and ecological function of wolves (e.g., MacNulty et al., 2014; Post et al., 1999). We encourage researchers to investigate the influence of variation in cohesion on components of individual fitness, population dynamics, and community-level (e.g., predator–prey, competition) interactions of social animals to evaluate the implications of differences in animal sociality associated with global change.

AUTHOR CONTRIBUTIONS

John F. Benson designed the research, initiated and led the collaboration, analyzed the data, and wrote the paper. David A. Keiter and Peter J. Mahoney prepared data for analysis and contributed to the analysis. All authors conducted fieldwork and contributed to revising the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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REFERENCES

Albery, G. F., A. Morris, S. Morris, J. M. Pemberton, T. H. Clutton-Brock, D. H. Nussey, and J. A. Firth. 2021. "Multiple Spatial Behaviours Govern Social Network Positions in a Wild Ungulate." *Ecology Letters* 24: 676–686.

Alexander, R. D. 1974. "The Evolution of Social Behavior." *Annual Review of Ecology, Evolution, and Systematics* 5: 325–383.

Aureli, F., C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, et al. 2008. "Fission-Fusion Dynamics: New Research Frameworks." *Current Anthropology* 49: 627–654.

Baan, C., R. Bergmüller, D. W. Smith, and B. Molnar. 2014. "Conflict Management in Free-Ranging Wolves, *Canis lupus*." *Animal Behaviour* 90: 327–334.

Barber-Meyer, S. M., and L. D. Mech. 2015. "Gray Wolf (*Canis lupus*) Dyad Monthly Association Rates by Demographic Group." *Canadian Wildlife Biology and Management* 4: 163–68.

Beale, C. M., J. J. Lennon, J. M. Yearsley, M. J. Brewer, and D. A. Elston. 2010. "Regression Analysis of Spatial Data." *Ecology Letters* 13: 246–264.

Bekoff, M. 1977. "Mammalian Dispersal and the Ontogeny of Individual Behavioral Phenotypes." *American Naturalist* 111: 715–732.

Bekoff, M., and M. C. Wells. 1980. "The Social Ecology of Coyotes." *Scientific American* 242: 130–151.

Benson, J. F., H. N. Abernathy, J. A. Sikich, and S. P. D. Riley. 2021. "Mountain Lions Reduce Movement, Increase Efficiency during the Covid-19 Shutdown." *Ecological Solutions and Evidence* 2: e12093.

Benson, J. F., K. M. Loveless, L. Y. Rutledge, and B. R. Patterson. 2017. "Ungulate Predation and Ecological Roles of Wolves and Coyotes in Eastern North America." *Ecological Applications* 27: 718–733.

Benson, J. F., and B. R. Patterson. 2013. "Moose (*Alces alces*) Predation by Eastern Coyotes (*Canis latrans*) and Eastern Coyote × Eastern Wolf (*Canis latrans × Canis lycaon*) Hybrids." *Canadian Journal of Zoology* 91: 837–841.

Benson, J. F., and B. R. Patterson. 2015. "Spatial Overlap, Proximity, and Habitat Use of Individual Wolves within the Same Packs." *Wildlife Society Bulletin* 39: 31–40.

Benson, J. F., B. R. Patterson, and T. J. Wheeldon. 2012. "Spatial Genetic and Morphologic Structure of Wolves and Coyotes in Relation to Environmental Heterogeneity in a *Canis* Hybrid Zone." *Molecular Ecology* 21: 5934–54.

Bracken, A. M., C. Christensen, M. J. O'Riain, I. Fürtbauer, and A. J. King. 2022. "Flexible Group Cohesion and Coordination, but Robust Leader–Follower Roles, in a Wild Social Primate Using Urban Space." *Proceedings of the Royal Society B* 289: 20212141.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, et al. 2008. "The Effects of Breeder Loss on Wolves". *The Journal of Wildlife Management* 72: 89–98.

Brown, J. L. 1974. "Alternate Routes to Sociality in Jays—With a Theory for the Evolution of Altruism and Communal Breeding." *American Zoologist* 14: 63–80.

Caraco, T., and L. L. Wolf. 1975. "Ecological Determinants of Group Sizes of Foraging Lions." *American Naturalist* 109: 343–352.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. "Energetic Constraints on the Diet of Terrestrial Carnivores." *Nature* 402: 286–88.

Cassidy, K. A., L. D. Mech, D. R. MacNulty, D. R. Stahler, and D. W. Smith. 2017. "Sexually Dimorphic Aggression Indicates Male Gray Wolves Specialize in Pack Defense against Conspecific Groups." *Behavioural Processes* 136: 64–72.

Chapman, C. A., L. J. Chapman, and R. W. Wrangham. 1995. "Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups." *Behavioral Ecology and Sociobiology* 36: 59–70.

Clutton-Brock, T. 2009. "Cooperation between Non-Kin in Animal Societies." *Nature* 462: 51–57.

Crabtree, R. L., and J. W. Sheldon. 1999. "The Ecological Role of Coyotes on Yellowstone's Northern Range." *Yellowstone Science* 7: 15–23.

Creel, S., and N. M. Creel. 1995. "Communal Hunting and Pack Size in African Wild Dogs, *Lycaon pictus*." *Animal Behavior* 50: 1325–39.

Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. "Density-Dependent Intraspecific Aggression Regulates Survival in Northern Yellowstone Wolves (*Canis lupus*)." *Journal of Animal Ecology* 83: 1344–56.

Doncaster, C. P., and D. W. Macdonald. 1997. "Activity Patterns and Interactions of Red Foxes (*Vulpes vulpes*) in Oxford City." *Journal of Zoology* 241: 73–87.

Dunbar, R. I., A. H. Korstjens, and J. Lemann. 2009. "Time as an Ecological Constraint." *Biological Reviews* 84: 413–429.

Fernandez-Sepulveda, J., and C. A. Martín. 2022. "Conservation Status of the World's Carnivorous Mammals (Order Carnivora)." *Mammalian Biology* 102: 1911–25.

Frid, A., and L. Dill. 2002. "Human-Caused Disturbance Stimuli as a Form of Predation Risk." *Conservation Ecology* 6(1): 11.

Fuller, T. K. 1989. "Population Dynamics of Wolves in North-Central Minnesota." *Wildlife Monographs* 105: 3–41.

Gable, T. D., S. K. Windels, J. G. Bruggink, and A. T. Homkes. 2016. "Where and how Wolves (*Canis lupus*) Kill Beavers (*Castor canadensis*)." *PLoS One* 11: e0165537.

Gable, T. D., S. K. Windels, M. C. Romanski, and F. Rosell. 2018. "The Forgotten Prey of an Iconic Predator: A Review of Interactions between Grey Wolves *Canis lupus* and Beavers *Castor* spp." *Mammal Review* 48: 123–138.

Gall, G. E., J. C. Evans, M. J. Silk, C. A. Ortiz-Jimenez, and J. E. Smith. 2022. "Short-Term Social Dynamics Following Anthropogenic and Natural Disturbances in a Free-Living Mammal." *Behavioral Ecology* 33: 705–720.

Gese, E. M. 2001. "Territorial Defense by Coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: Who, How, Where, When, and Why." *Canadian Journal of Zoology* 79: 980–87.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. "Relationship between Coyote Group Size and Diet in Southeastern Colorado." *The Journal of Wildlife Management* 52: 647–653.

Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. "Social and Nutritional Factors Influencing the Dispersal of Resident Coyotes." *Animal Behaviour* 52: 1025–43.

Giraldeau, L.-A., and T. Caraco. 2000. *Social Foraging Theory.* Princeton, NJ: Princeton University Press.

Goldenberg, S. Z., I. Douglas-Hamilton, and G. Wittemyer. 2016. "Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks." *Current Biology* 26: 75–79.

Harrison, D. J., J. A. Harrison, and M. O'Donoghue. 1991. "Predispersal Movements of Coyote (*Canis latrans*) Pups in Eastern Maine." *Journal of Mammalogy* 72: 756–763.

IPCC. 2021. *Climate Change 2021: The Physical Science Basis. Summary for Policymakers. Contribution of the Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge: Cambridge University Press.

Jensen, A. J., C. J. Marneweck, J. C. Kilgo, and D. S. Jachowski. 2022. "Coyote Diet in North America: Geographic and Ecological Patterns during Range Expansion." *Mammal Review* 52: 480–496.

jfbenson22. 2024. "jfbenson22/CanisCohesion: Initial Release (0.1.0)." Zenodo. https://doi.org/10.5281/zenodo.13891913.

Jordan, N. R., K. A. Golabek, D. M. Behr, R. H. Walker, L. Plimpton, S. Lostrom, M. Classe, L. K. Van der Weyde, and J. W. McNutt. 2022. "Priority of Access to Food and Its Influence on Social Dynamics of an Endangered Carnivore." *Behavioral Ecology and Sociobiology* 76: 1–15.

Josi, D., A. Freudiger, M. Taborsky, and J. G. Frommen. 2020. "Experimental Predator Intrusions in a Cooperative Breeder Reveal Threat-Dependent Task Partitioning." *Behavioral Ecology* 31: 1369–78.

Kamler, J. F., and D. W. Macdonald. 2014. "Social Organization, Survival, and Dispersal of Cape Foxes (*Vulpes chama*) in South Africa." *Mammalian Biology* 79: 64–70.

Kappeler, P. M., and C. P. van Schaik. 2002. "Evolution of Primate Social Systems." *International Journal of Primatology* 23: 707–740.

Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker. 2019. "Managing the

Middle: A Shift in Conservation Priorities Based on the Global Human Modification Gradient." *Global Change Biology* 25: 811–826.

Kitchen, A. M., E. M. Gese, L. P. Waits, S. M. Karki, and E. R. Schauster. 2005. "Genetic and Spatial Structure within a Swift Fox Population." *Journal of Animal Ecology* 74: 1173–81.

Komdeur, J., and L. Ma. 2021. "Keeping Up with Environmental Change: The Importance of Sociality." *Ethology* 127: 790–807.

Krause, J., and G. D. Ruxton. 2002. *Living in Groups.* Oxford: Oxford University Press.

Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2007. "Group Size, Grooming, and Social Cohesion in Primates." *Animal Behaviour* 74: 1617–29.

Lesmerises, F., C. Dussault, and M. H. St-Laurent. 2012. "Wolf Habitat Selection Is Shaped by Human Activities in a Highly Managed Boreal Forest." *Forest Ecology and Management* 276: 125–131.

Lima, S. L., and L. M. Dill. 1990. "Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus." *Canadian Journal of Zoology* 68: 619–640.

Liu, J., X. Ma, Z. Duan, J. Jiang, M. Reichstein, and M. Jung. 2020. "Impact of Temporal Precipitation Variability on Ecosystem Productivity." *Wiley Interdisciplinary Reviews Water* 7: e1481.

Lusseau, D., and M. E. Newman. 2004. "Identifying the Role that Animals Play in Their Social Networks." *Proceedings of the Royal Society of London B: Biological Sciences* 271: S477–S481.

MacNulty, D. R., D. W. Smith, L. D. Mech, and L. E. Eberly. 2009. "Body Size and Predatory Performance in Wolves: Is Bigger Better?" *Journal of Animal Ecology* 78: 532–39.

MacNulty, D. R., A. Tallian, D. R. Stahler, and D. W. Smith. 2014. "Influence of Group Size on the Success of Wolves Hunting Bison." *PLoS One* 9: e112884.

Marty, P. R., B. Beisner, S. S. Kaburu, K. Balasubramaniam, E. Bliss-Moreau, N. Ruppert, S. A. M. Sah, et al. 2019. "Time Constraints Imposed by Anthropogenic Environments Alter Social Behaviour in Longtailed Macaques." *Animal Behaviour* 150: 157–165.

Mbizah, M. M., D. R. Farine, M. Valeix, J. E. Hunt, D. W. Macdonald, and A. J. Loveridge. 2020. "Effect of Ecological Factors on Fine-Scale Patterns of Social Structure in African Lions." *Journal of Animal Ecology* 89: 2665–76.

Mech, L. D., and L. Boitani. 2003. "Wolf Social Ecology." In *Wolves: Behavior, Ecology, and Conservation*, edited by L. Mech and L. Boitani, 1–34. Chicago, IL: University of Chicago Press.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. "Interference Competition between Gray Wolves and Coyotes in Yellowstone National Park." *Canadian Journal of Zoology* 87: 56–63.

Messier, F. 1985. "Social Organization, Spatial Distribution, and Population Density of Wolves in Relation to Moose Density." *Canadian Journal of Zoology* 65: 1068–77.

Metz, M. C., J. A. Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. "Effect of Sociality and Season on Gray Wolf (*Canis lupus*) Foraging Behavior: Implications for Estimating Summer Kill Rate." *PLoS One* 6: e17332.

Mosser, A., and C. Packer. 2009. "Group Territoriality and the Benefits of Sociality in the African Lion, *Panthera leo*." *Animal Behaviour* 78: 359–370.

Nickel, B. A., J. P. Suraci, A. C. Nisi, and C. C. Wilmers. 2021. "Energetics and Fear of Humans Constrain the Spatial Ecology of Pumas." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2004592118.

Nordli, K., P. Wabakken, A. Eriksen, H. Sand, C. Wikenros, E. Maartmann, and B. Zimmermann. 2023. "Spatial and Temporal Cohesion of Parents and Offspring in a Social Large Carnivore." *Animal Behaviour* 197: 155–167.

Oliveira, T., J. F. Benson, C. Thompson, and B. R. Patterson. 2020. "Resource Selection at Homesites by Wolves and Eastern Coyotes in a *Canis* Hybrid Zone." *Ecosphere* 11: e03320.

Ordiz, A., C. Milleret, J. Kindberg, J. Månsson, P. Wabakken, J. E. Swenson, and H. Sand. 2015. "Wolves, People, and Brown Bears Influence the Expansion of the Recolonizing Wolf Population in Scandinavia." *Ecosphere* 6: 1–14.

Patterson, B. R., and F. Messier. 2001. "Social Organization and Space Use of Coyotes in Eastern Canada Relative to Prey Distribution and Abundance." *Journal of Mammalogy* 82: 463–477.

Peterson, R. O., and P. Ciucci. 2003. "The Wolf as a Carnivore." In *Wolves: Behavior, Ecology, and Conservation*, edited by L. Mech and L. Boitani, 104–130. Chicago, IL: University of Chicago Press.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. "Wolves of the Kenai Peninsula, Alaska." *Wildlife Monographs* 88: 3–52.

Pollard, K. A., and D. T. Blumstein. 2008. "Time Allocation and the Evolution of Group Size." *Animal Behaviour* 76: 1683–99.

Port, M., P. M. Kappeler, and R. A. Johnstone. 2011. "Communal Defense of Territories and the Evolution of Sociality." *American Naturalist* 178: 787–800.

Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. "Ecosystem Consequences of Wolf Behavioural Response to Climate." *Nature* 401: 905–7.

Ralls, K., B. Cypher, and L. K. Spiegel. 2007. "Social Monogamy in Kit Foxes: Formation, Association, Duration, and Dissolution of Mated Pairs." *Journal of Mammalogy* 88: 1439–46.

Rio-Maior, H., P. Beja, M. Nakamura, and F. Álvares. 2018. "Use of Space and Homesite Attendance by Iberian Wolves during the Breeding Season." *Mammalian Biology* 92: 1–10.

Rio-Maior, H., M. Nakamura, F. Álvares, and P. Beja. 2019. "Designing the Landscape of Coexistence: Integrating Risk Avoidance, Habitat Selection and Functional Connectivity to Inform Large Carnivore Conservation." *Biological Conservation* 235: 178–188.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, et al. 2014. "Status and Ecological Effects of the World's Largest Carnivores." *Science* 343(6167): 1241484.

Robert, K., D. Garant, and F. Pelletier. 2012. "Keep in Touch: Does Spatial Overlap Correlate with Contact Rate Frequency?" *Journal of Wildlife Management* 76: 1670–75.

Robinson, T. M., K. J. La Pierre, M. A. Vadeboncoeur, K. M. Byrne, M. L. Thomey, and S. E. Colby. 2013. "Seasonal, Not Annual Precipitation Drives Community Productivity across Ecosystems." *Oikos* 122: 727–738.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. "Effects of Hunting Group Size, Snow Depth and Age on the Success of Wolves Hunting Moose." *Animal Behaviour* 72: 781–89.

Sells, S. N., M. S. Mitchell, K. M. Podruzny, D. E. Ausband, D. J. Emlen, J. A. Gude, T. D. Smucker, et al. 2022. "Competition, Prey, and Mortalities Influence Gray Wolf Group Size." *Journal of Wildlife Management* 86: e22193.

Silk, J. B. 2007. "The Adaptive Value of Sociality in Mammalian Groups." *Philosophical Transactions of the Royal Society B: Biological Sciences* 362: 539–559.

Smith, J. E., J. M. Kolowski, K. E. Graham, S. E. Dawes, and K. E. Holekamp. 2008. "Social and Ecological Determinants of Fission–Fusion Dynamics in the Spotted Hyaena." *Animal Behaviour* 76: 619–636.

Smith-Aguilar, S. E., G. Ramos-Fernández, and W. M. Getz. 2016. "Seasonal Changes in Socio-Spatial Structure in a Group of Free-Living Spider Monkeys (*Ateles geoffroyi*)." *PLoS One* 11: e0157228.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Taborsky, M., M. A. Cant, and J. Komdeur. 2021. *The Evolution of Social Behaviour*. Cambridge: Cambridge University Press.

Thomson, P. C. 1992. "The Behavioural Ecology of Dingoes in North-Western Australia. IV. Social and Spatial Organisation, and Movements." *Wildlife Research* 19: 543–563.

Vucetich, J. A., R. O. Peterson, and T. A. Waite. 2004. "Raven Scavenging Favours Group Foraging in Wolves." *Animal Behaviour* 67: 1117–26.

Walton, Z., G. Samelius, M. Odden, and T. Willebrand. 2018. "Long-Distance Dispersal in Red Foxes *Vulpes vulpes* Revealed by GPS Tracking." *European Journal of Wildlife Research* 64: 64.

Warton, D. I., and F. K. Hui. 2011. "The Arcsine Is Asinine: The Analysis of Proportions in Ecology." *Ecology* 92: 3–10.

Wells, J. V., N. Dawson, N. Culver, F. A. Reid, and S. Morgan Siegers. 2020. "The State of Conservation in North America's Boreal Forest: Issues and Opportunities." *Frontiers in Forests and Global Change* 3: 90.

Wey, T. W., and D. T. Blumstein. 2010. "Social Cohesion in Yellow-Bellied Marmots Is Established through Age and Kin Structuring." *Animal Behaviour* 79: 1343–52.

Wey, T. W., J. R. Burger, L. A. Ebensperger, and L. D. Hayes. 2013. "Reproductive Correlates of Social Network Variation in Plurally Breeding Degus (*Octodon degus*)." *Animal Behaviour* 85: 1407–14.

Wiszniewski, J., S. J. Allen, and L. M. Möller. 2009. "Social Cohesion in a Hierarchically Structured Embayment Population of Indo-Pacific Bottlenose Dolphins." *Animal Behaviour* 77: 1449–57.

Wittemyer, G., I. Douglas-Hamilton, and W. M. Getz. 2005. "The Socioecology of Elephants: Analysis of the Processes Creating Multitiered Social Structures." *Animal Behaviour* 69: 1357–71.

Wood, S. N. 2006. *Generalized Additive Models: An Introduction with R*. Boca Raton, FL: Taylor Francis.

Wood, S. N., and N. H. Augustin. 2002. "GAMs with Integrated Model Selection Using Penalized Regression Splines and Applications to Environmental Modelling." *Ecological Modelling* 157: 157–177.

Wrangham, R. W. 1980. "An Ecological Model of Female-Bonded Primate Groups." *Behaviour* 75: 262–300.

Zhang, W., K. Furtado, P. Wu, T. Zhou, R. Chadwick, C. Marzin, J. Rostron, and D. Sexton. 2021. "Increasing Precipitation Variability on Daily-to-Multiyear Time Scales in a Warmer World." *Science Advances* 7: eabf8021.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.