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LETTER

# Denning phenology and reproductive success of wolves in response to climate signals

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Supplementary material for this article is available online

## Abstract

Arctic and boreal ecosystems are experiencing rapid changes in temperature and precipitation regimes. Subsequent shifts in seasonality can lead to a mismatch between the timing of resource availability and species' life-history events, known as phenological or trophic mismatch. Although mismatch has been shown to negatively affect some northern animal populations, longer-term impacts across large regions remain unknown. In addition, animals may rely on climate cues during preceding seasons to time key life history events such as reproduction, but the reliability of these cues as indicators of subsequent resource availability has not been examined. We used remote sensing and gridded spatial data to evaluate the effect of climate factors on the reproductive phenology and success of a wide-ranging carnivore, the gray wolf (*Canis lupus*). We used global positioning system (GPS) location data from 388 wolves to estimate den initiation dates ($n = 227$ dens within 106 packs) and reproductive success in eight populations across northwestern North America from 2000 to 2017. Spring onset shifted 14.2 d earlier, on average, during the 18-year period, but the regional mean date of denning did not change. Preceding winter temperature was the strongest climatic predictor of denning phenology, with higher temperatures advancing the timing of denning. Winter temperature was also one the strongest and most reliable indicators of the timing of spring onset. Reproductive success was not affected by timing of denning or synchrony with spring onset, but improved during cooler summers and following relatively dry autumns. Our findings highlight a disconnect between climate factors that affect phenology and those that affect demography, suggesting that carnivores may be resilient to shifts in seasonality and yet sensitive to weather conditions affecting their prey at both local and regional scales. These insights regarding the relationship between climate and carnivore demography should improve predictions of climate warming effects on the highest trophic levels.

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## 1. Introduction

Phenological responses to climate are pervasive in the natural world (Stenseth and Mysterud 2002, Thackeray *et al* 2010, 2016). Annual cycles characterized by changes in temperature, precipitation, and hydrology can drive temporal patterns in nutrient availability and resource distribution, with profound effects on habitat suitability (Parmesan 2006, Chen *et al* 2011), species demography (Regehr *et al* 2007, Inman *et al* 2012, Stirling and Derocher 2012), and community composition (Walther *et al* 2002, Henry and Molau 2003, Ovaskainen *et al* 2013). Individuals that time resource-limited life history events to coincide with peak resource availability should accrue fitness benefits relative to those who do not (Parker *et al* 2009, Thackeray *et al* 2010, 2016, Boutin and Lane 2014). Thus, the consequences of phenological asynchrony with optimal conditions due to changing environments is a major conservation concern. The demographic repercussions of phenological mismatch have been documented for several wildlife species at lower trophic levels (Miller-Rushing *et al* 2010, Thackeray *et al* 2010), but the impacts of climate variability on large carnivores are not well understood. The fundamental role of large carnivores in shaping communities suggests this deficiency may limit our understanding of how future climate change will impact community stability and species viability (Miller-Rushing *et al* 2010, Wilmers *et al* 2012, Winnie and Creel 2017).

Weather may signal changes in resources vital to reproduction. Reproduction is likely sensitive to weather conditions due to the considerable increase in energy requirements associated with offspring development and in some cases, post-parturition parental care (Oftedal and Gittleman 1989). Reproduction often requires preparatory actions, both behavioral (e.g. courtship) and physiological (e.g. dormancy, incubation, and gestation), that can create a temporal disconnect between climate signals at the onset of reproduction and resource pulses around the time of parturition (Both *et al* 2009, Gienapp *et al* 2014). Thus, the ability to match optimal conditions for rearing offspring may reflect selective pressures acting on breeding phenology and fitness following parturition (Kerby and Post 2013). In seasonal systems where optimal conditions are ephemeral, the abiotic environments that are within the physiological tolerances of neonates and that affect the temporal variability in prey availability, vulnerability, and predictability are likely to affect the extent to which carnivore reproductive phenology responds to climate signals (Both *et al* 2009, Inman *et al* 2012, Gienapp *et al* 2014).

Although some species may adjust their timing of parturition in response to weather cues, the degree of seasonality and magnitude of cross-seasonal correlations in weather are likely to influence the predictability of resource pulses (Colwell 1974) and therefore, the extent to which species respond to climate cues. If seasonal conditions are highly correlated (e.g. mild winters associated with mild springs, or early autumns associated with early springs), species may modify breeding phenology in response to climate cues during the breeding season that signal optimal weather conditions for parturition or offspring development. If seasons are weakly correlated, then climate cues during the breeding season would be unreliable indicators of the climatic state during the offspring rearing period, and species would not be expected to adjust timing of breeding in response to weather variability. To examine the potential value of breeding season conditions as indicators of offspring rearing conditions, we examined inter-seasonal correlations in weather during our 18-year study period. We also examined whether the level of inter-seasonal correlation has changed over time to determine whether previously strong climate indicators are breaking down with climate change.

Here, we examined the influence of climate on gray wolf (*Canis lupus*) reproduction from 2000 to 2017. As one of the most well-studied and widespread apex predators, gray wolves are an ideal candidate for investigating climate drivers in carnivore reproduction. With an extended gestation of approximately nine weeks (62 $\pm$ 3 d), wolves breed in the winter and give birth in the spring with a high degree of synchrony across social units (i.e. packs) within populations (Asa and Valdespino 1998, Mech and Boitani 2010). Although very little is known about the underlying mechanisms associated with the timing of wolf reproduction, the synchrony in spring parturition, as well as the observed delay in parturition at higher elevations (Joly *et al* 2018) and latitudes (Mech and Boitani 2010), indicate strong selective pressures acting on wolf denning phenology with possible cuing by climate signals. Therefore, we evaluated potential climate mechanisms underlying two components of grey wolf reproduction using a large regional dataset from North America (tables 1 and 2). We specifically assessed whether prior environmental conditions influenced the timing of natal den initiation (i.e. phenology), and whether past or contemporary environmental conditions influenced reproductive success (i.e. presence of one or more pups at the end of August) in wolves. Our findings pertaining to the effects of climate on the demography of wolves will likely have important implications for numerous sympatric species worldwide.

## 2. Materials and methods

### 2.1. Study domain

We compiled GPS location data from 388 individuals in eight wolf populations across western Canada and

**Table 1.** The hypothetical mechanisms by which climate influences wolf denning phenology and reproductive success. These hypotheses were used to justify the climate covariates used in each analysis. *t-1* indicates the season prior to the denning event.

| Season | Mechanism | Predictions |
|---|---|---|
| *Denning phenology* | | |
| $Spring_{t-1}$ | Past experience may inform spring onset the following year, particularly with strong correlation between past and current spring conditions | Later SOS during the previous spring will promote later denning in the current year. |
| $Summer_{t-1}$ | Summer growing season conditions may influence female ungulate condition, timing of ungulate estrus, and overwinter wolf condition, potentially affecting wolf breeding phenology | Longer and more productive growing seasons (LOS, tiNDVI), as well as higher temperatures, will promote earlier denning |
| $Autumn_{t-1}$ | Autumn conditions influencing rut phenology in ungulates may cue wolf pair formation and breeding in the winter | Lower temperatures and higher precipitation totals in the autumn will delay wolf denning |
| $Winter_{t-1}$ | Winter conditions may affect the timing of pair formation/disruption and female condition in wolves, potentially driving the timing of estrus | Lower temperatures and higher snow water equivalent (SWE) in the winter will delay wolf denning |
| Decadal cycles | Longer term, regional climate patterns may influence prey populations states, influencing prey vulnerability and availability | High snowfall years in PDO/AO cycles will delay wolf denning |
| *Reproductive success* | | |
| $Autumn_{t-1}$ | Autumn conditions affect the abundance and condition of prey from winter through pup rearing, thereby affecting female wolf body condition through the early stages of reproduction | Higher Autumn temperatures with less precipitation will improve reproductive success |
| $Winter_{t-1}$ | Winter conditions may influence prey availability and vulnerability, thereby affecting female wolf body condition through the early stages of reproduction | More winter precipitation and higher snow water equivalent (SWE) will improve reproductive success |
| Spring | Parturition phenology and synchrony with SOS may influence availability of vulnerable prey when caloric demands are highest for lactating mothers and developing young, thereby influencing wolf reproductive success | Higher synchronicity between wolf denning and SOS will improve reproductive success |
| Summer | Summer climatic conditions may influence prey abundance, availability, and susceptibility to predation. Temperatures and precipitation may influence time spent hunting in wolves as a coursing predator | Longer, more productive growing seasons (LOS, tiNDVI) and cooler temperatures will improve reproductive success |
| Decadal cycles | Longer term, regional climate patterns may influence prey populations states, influencing prey vulnerability and availability | Warmer and wetter years in PDO/AO cycles will increase reproductive success |

**Table 2.** The centroid location, number of pack-years (N), and monitoring periods used in an assessment of grey wolf denning phenology and reproductive success partitioned by study.

| Study | Longitude | Latitude | Denning phenology (N) | Reproductive success (N) | Years |
|---|---|---|---|---|---|
| Gwich'in NRB, NWT, CA | −135.76367 | 67.83620 | 3 | 3 | 2007–2007 |
| Yukon-Charley Rivers NPP, Alaska, USA | −143.22796 | 65.04694 | 63 | 57 | 2003–2015 |
| Denali NP, Alaska, USA | −150.48638 | 63.63523 | 85 | 76 | 2004–2016 |
| ADFG Nelchina PUA, Alaska, USA | −146.81178 | 62.40836 | 10 | 7 | 2000–2005 |
| Great Slave Lake, NWT, CA | −116.11118 | 60.88060 | 7 | 6 | 2016–2017 |
| Lake Clark NP, Alaska, USA | −154.58120 | 60.49529 | 11 | 8 | 2009–2013 |
| West Athabasca River, Alberta, CA | −112.96679 | 55.85988 | 8 | 5 | 2006–2007 |
| Jasper-Banff NP, Alberta-BC, CA | −117.69928 | 52.97055 | 40 | 24 | 2000–2011 |

Alaska (figure 1) (Longitude: −154.6 to −112.7°, Latitude: 51.5 to 67.8°; table 2). Wolves were captured following standard animal care protocols defined by affiliate university or government agencies and released with GPS collars programmed to acquire fixes over a range of intervals from 15 min to 24 h. Each population was monitored from 1 to 12 years between 2000 and 2017.

### 2.2. Wolf denning phenology and reproductive success

The movements and site-fidelity patterns of resident pack members can signal pup-rearing activities from March through August (Alfredéen 2006, Tsunoda *et al* 2009). These patterns emerge from food provisioning and other social interactions that regularly draw pack members back to pup-rearing sites that serve

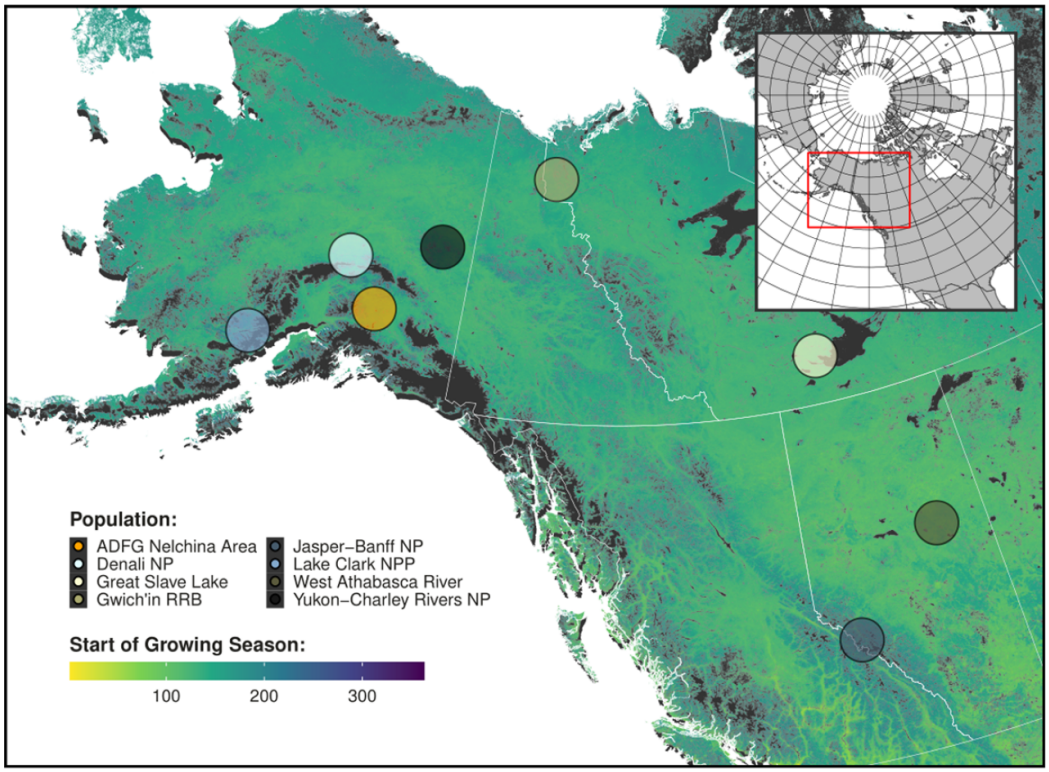


**Figure 1.** Spatial distribution of eight wolf study populations used in an assessment of denning phenology in response to climate signals (2000–2017). The base map shows the day of year representing the NDVI-derived start of growing season in 2010.

as social centers throughout the summer (i.e. dens and rendezvous sites) (Ballard *et al* 1991, Alfredéen 2006, Ciucci and Mech 2006). Thus, the movements of non-reproductive individuals can be as informative as reproductive individuals (Tsunoda *et al* 2009).

We classified movements indicative of pup rearing using a three-step process. For the first step, we identified sites with a high-intensity of use by clustering collared animal locations in space (⩽100 m) and time (⩽7 d) (R package rASF (Mahoney and Young 2017)). This process is performed iteratively over all locations within an animal's truncated time series, producing convex hulls for each set of points that meet the criteria. We then merged all overlapping convex hulls (in space and time) into a single cluster and removed any clusters with fewer than eight locations (or five for 24 h fix interval datasets). For the second step, we smoothed the same movement time series using a median filter and an overlapping, 4 d moving window to dampen the effect of large movements. We flagged 4 d periods with median daily displacements less than 200 m and overlaid the output on our cluster data. For the final step, we visually inspected movement time series to evaluate whether cluster fidelity persisted after frequent offsite forays (i.e. provisioning of offspring) and to identify any influential gaps in location data that could affect estimates for den initiation dates (figure 2). We estimated parturition as the initial date from the earliest denning cluster observed during the reported period for wolf parturition (March–June; Mech and Boitani 2010). Occasionally, movement data from a reproductive female expressed gaps in a location time series that lasted approximately 4 d to 8 d, an indication of GPS satellite signal occlusion while in underground dens (Joly *et al* 2018). Visual inspection of the time series helped to identify these gaps so that den initiation dates (i.e. parturition dates) could be adjusted to when the signal was first lost. However, in cases where denning initiation were unclear, particularly for known non-breeding individuals, the movement data were removed from further consideration.

We define reproductive success as packs with one or more pups at the end of August. To estimate success, we evaluated the movement time series for each individual after a denning event had been identified. If pup-rearing movements were evident through the end of August using the same methods above (e.g. high-fidelity clusters and low daily median displacement through August), we flagged these packs as reproductively successful. Although these activities often extended well into September or October, we chose August as a more conservative date given the variability in when pups begin to consistently travel with natal packs. We validated success by comparing our estimates to visual observations of pups with packs during the autumn or winter for a portion of our dataset for which these observations were made (Denali National Park and Preserve, Banff National Park, Jasper National Park, and West Athabasca River study areas).

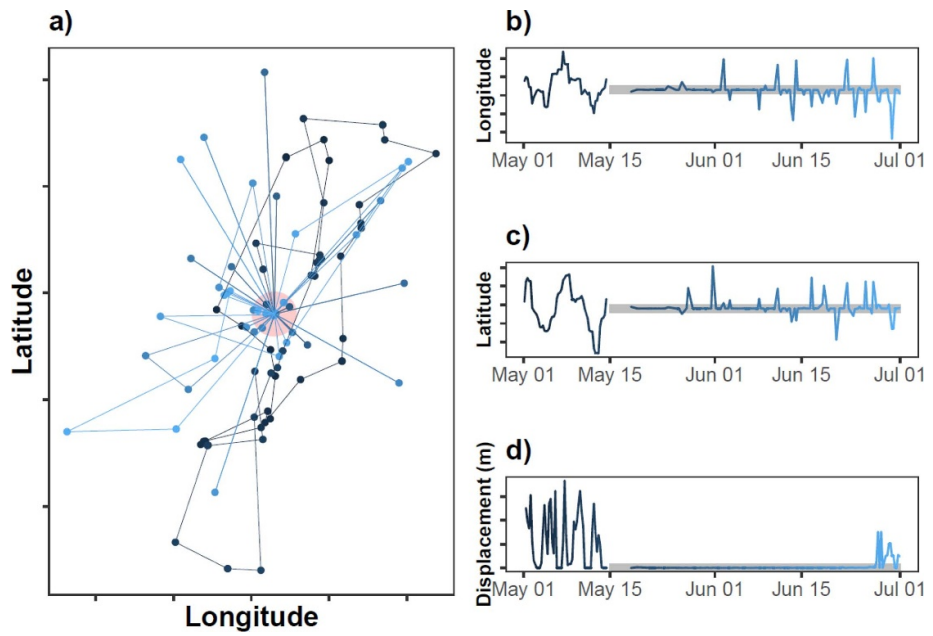


**Figure 2.** A visual depiction of the approach used to characterize wolf den and rendezvous sites using a combination of spatial clustering and confined median daily displacements. Each point (a) and line (a)–(d) correspond to a median daily location and displacement between consecutive locations, respectively, for a single reproductive female. All points and displacements are colored by time from dark blue (early) to light blue (late). The red circle in (a) indicates a den site with characteristic web-like movements. The gray semi-opaque band in (b)–(d) highlights the timing and duration of an individual's denning activity. Further, the 4 d gap in locations depicted at the start of the denning period was due to the collars inability to acquire satellite signals when in a den, often a tell-tale for den initiation in collared females.

In addition, because we performed these assessments for each individual independent of pack membership, we used pack members as a form of validation in our estimates for both den initiation and reproductive success. However, for the analyses below, we used only one estimate of reproductive timing and success per pack per year, prioritizing dates derived from reproductive females followed by individuals with the highest quality data (i.e. highest fix retention or sampling rate).

### 2.3. Climate metrics

We aggregated seasonal weather metrics using Daymet (v3; Thornton *et al* 2018), a meteorological product that contains daily estimates for minimum and maximum temperatures, total precipitation, and snow water equivalent (SWE) on a global 1 km grid. To characterize vegetation dynamics during the most photosynthetically active periods (i.e. growing season), we estimated Normalized Difference Vegetation Index using 8 d surface reflectance derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS; MOD09Q1 data product, ORNL DAAC 2017). We post-processed NDVI data using the program TIMESAT (Jönsson and Eklundh 2004), which masked cloud-covered pixels, smoothed NDVI time series, and estimated phenological metrics such as start of growing season (SOS), length of growing season (LOS), and time-integrated NDVI (tiNDVI). We defined growing season start and end dates by when pixels passed the 10% and 90% thresholds for mean NDVI amplitude as measured across a seasonal time series. We estimated snow disappearance date (SDD), or the first snow free day after a minimum of 3 d with snow cover (assessed backwards in time to capture the end of the snow-covered season), using the MODIS normalized snow difference index (MOD10A1; Hall *et al* 2006) and the Google Earth Engine API. We also included PDO (http://jisao.washington.edu/pdo; Mantua and Hare 2002) and Arctic Oscillation indices (AO) (NOAA National Weather Service Climate Prediction Center; www.cpc.ncep.noaa.gov) during January of the reproductive year and annual means from the previous year (effectively, a lag of one year; figure 3(b)). See table 3 for a complete description of each covariate.

To define local domains for weather conditions, we calculated seasonal wolf home ranges using 95% isopleths from fixed-kernel density estimates (Sheather and Jones 1991). We defined three biological seasons: summer (pup-rearing: April–August), autumn (ungulate rut: September–November), and winter (wolf pair formation and breeding: January–March). We used seasonal home ranges to extract median climate statistics, and home range centroids to estimate latitude for each individual. In the absence of wolf movement data during any non-denning seasons, summer home ranges summaries were used instead given the strong seasonal site fidelity exhibited by wolves (Mech and Boitani 2010).

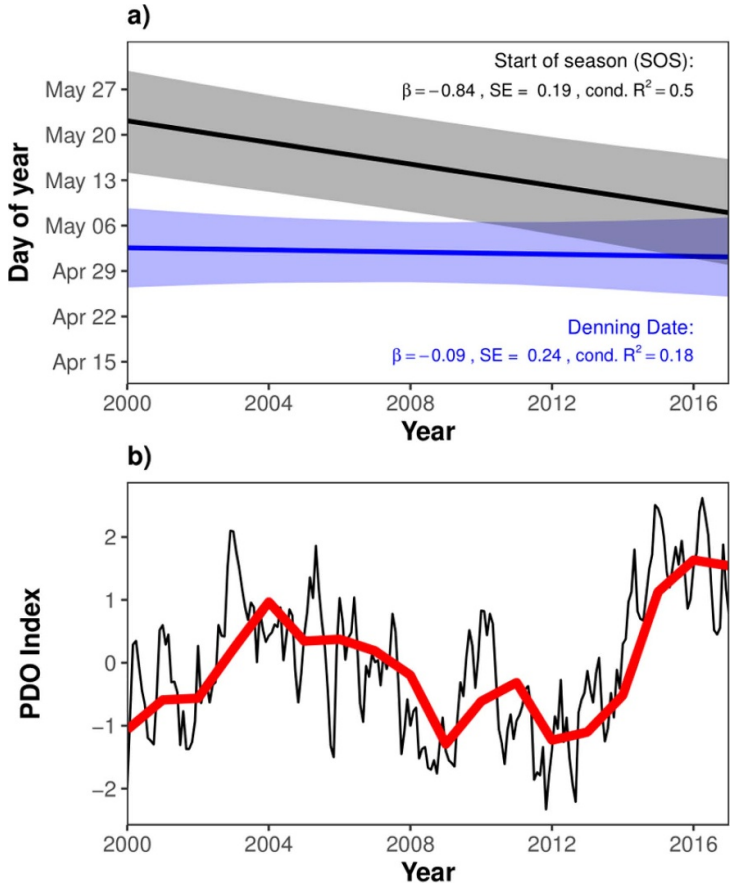


**Figure 3.** Linear regression model fit for start of growing season (SOS, black line with gray 95% CI band) and marginal denning date (all populations, blue line and 95% CI band) (a). The PDO index (b) plotted as monthly means (black line) and annual means (red) during the study period (2000–2017).

**Table 3.** Variable descriptions for all covariates used in an assessment of wolf denning phenology and reproductive success. Values represent summaries across all records, and therefore all study systems and years, within the complete dataset (i.e. reproductive phenology dataset). The mean and standard deviations displayed here were used to standardize covariates prior to model fitting.

| Covariate | Full Name | Mean | Standard deviation | Minimum | Maximum |
|---|---|---|---|---|---|
| Sync_SOS | Denning date synchrony with SOS (d) | 0.00 | 20.81 | −59.47 | 43.45 |
| SOS | Start of growing season (Day of Year) | 137.88 | 14.70 | 101.95 | 177.31 |
| tiNDVI | Time-integrated NDVI | 12.04 | 3.10 | 4.36 | 31.49 |
| LOS | Length of growing season (d) | 18.59 | 3.04 | 10.53 | 31.31 |
| January_PDO | January Pacific Decadal Oscillation Index | 0.18 | 1.12 | −2.00 | 2.45 |
| Annual_PDO | Annual Pacific Decadal Oscillation Index | −0.08 | 0.85 | −1.29 | 1.63 |
| January_AO | January Arctic Oscillation Index | −0.21 | 1.38 | −2.59 | 2.03 |
| Annual_AO | Annual Arctic Oscillation Index | −0.03 | 0.41 | −1.04 | 0.63 |
| Autumn_TMIN | Median autumn daily minimum temperature (°C) | −5.90 | 2.95 | −14.00 | 0.00 |
| Autumn_TMAX | Median autumn daily maximum temperature (°C) | 1.48 | 3.30 | −7.00 | 10.00 |
| Autumn_PRCP | Autumn total precipitation (mm) | 133.30 | 70.49 | 23.00 | 442.00 |
| Winter_TMIN | Median winter daily minimum temperature (°C) | −18.68 | 5.41 | −30.00 | −8.00 |
| Winter_TMAX | Median winter daily maximum temperature (°C) | −7.64 | 5.27 | −23.00 | 3.00 |
| Winter_SWE | Winter daily snow water equivalent | 90.38 | 53.10 | 12.00 | 404.00 |
| Summer_TMIN | Median summer daily minimum temperature (°C) | 5.91 | 2.14 | −3.00 | 11.00 |
| Summer_TMAX | Median summer daily maximum temperature (°C) | 17.35 | 2.75 | 11.00 | 24.00 |
| Summer_PRCP | Summer total precipitation (mm) | 257.23 | 94.96 | 44.00 | 518.00 |
| SDD | Snow disappearance date (Day of Year) | 125.76 | 16.47 | 94.00 | 232.00 |

### 2.4. Analyses

Prior to the analyses, we assessed collinearity across all covariates and removed one or more covariates that contributed to correlation coefficients greater than 0.7. In cases where correlation occurred, we retained the metric that best represented the underlying, hypothesized biological mechanisms. We also evaluated temporal trends in median SOS and denning date during the years for which we had wolf denning data by fitting linear mixed effects model with either SOS or denning date as the response variable, a single continuous effect of year, and random intercepts for study system. We estimated shifts in dates based on predictions derived from models with significant effects of year (95% confidence interval for year did not overlap zero).

Next, we evaluated inter-seasonal correlations (figure 1). We defined population domains by their minimum convex polygons (MCP; Calenge 2006) using all collared individuals within a population. For each population domain, we estimated median SOS, seasonal temperatures, cumulative precipitation, and SWE across all years within the study (2000–2017). We then generated population-specific Pearson's correlation coefficients by pairing SOS with climate metrics from the previous winter, autumn, and summer during each year, thus producing annual estimates of correlation for each climate metric by population across all years.

We used a time-to-event model, Cox proportional hazard regression (R package survival, Therneau 2015), to examine the effects of climate factors on denning phenology. Denning phenology was measured as the number of calendar days since January 1st and the initiation date of each documented denning event. The baseline 'hazard' in this context reflected the daily probability of denning from January through the middle of June. We derived robust, Huber sandwich variance estimates to account for non-independence in the timing of denning for packs with more than one denning event across multiple years (i.e. specified 'cluster(PackID)' in the model formulation; Therneau 2015). We evaluated the influence of seasonal (previous summer, autumn, and winter) minimum and maximum temperatures, previous summer and autumn cumulative precipitation, mean daily SWE, SDD, SOS, LOS, tiNDVI, latitude, annual PDO, and annual AO on the timing of wolf den initiation.

We assessed climatic factors affecting reproductive success using mixed logistic regression with success (1) and failure (0) as a binary response (R package lme4; Bates 2010). We included random intercepts for pack nested within population and evaluated the influence of synchrony with spring onset (i.e. the difference between denning date and start of growing season), annual PDO (previous year), seasonal weather conditions, and time-integrated tiNDVI. In contrast to the phenology analyses, summer conditions were based on the current reproductive year rather than from the previous summer. In addition to a linear effect of spring onset, we considered a non-linear second-order polynomial and a linear piecewise response to synchrony with spring onset (i.e. using a single knot at 0 representing perfect synchrony) to account for possible differences in success whether litters were born before or after spring onset. We also included summer home range area ($km^2$) as an indirect measure of home range quality, because smaller home ranges are often associated with higher resource productivity (Duncan *et al* 2015).

We standardized all covariates by centering on the mean and dividing by one standard deviation prior to modeling (Gelman *et al* 2014). We ran all-possible additive models using the R package MuMIn (Barton 2009). Models were ranked by Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). We generated model-averaged coefficient estimates and confidence intervals based on unconditional standard errors following Burnham and Anderson (2002). Model-averaged coefficient estimates were derived across all models, but the estimate for any particular covariate was conditional on its presence within a model (i.e. coefficients were not fixed at 0 when absent). We determined variable importance using parameter weights (Burnham and Anderson 2002) and confidence interval overlap with zero (85% level; Arnold 2010). We also evaluated both model sets for uninformative parameters using personally authored R code (*sensu* Leroux 2019), which we retained when deriving parameter weights (to achieve covariate balance across model sets; Burnham and Anderson 2002) and model-averaged estimates in an all possible models context (Arnold 2010).

We assessed model goodness-of-fit by using the Cox proportional hazard concordance statistic for the denning phenology model set (Therneau 2015) and conditional pseudo-$R^2$ for the reproductive success model set (Nakagawa *et al* 2017). Concordance is a measure of agreement between observed and predicted values commonly used in time-to-event models (Therneau 2015). This is accomplished by ranking the 'risk' scores (exponentiated linear predictor in a hazard model) of a pack at each observed denning event relative to all packs who have yet to den. Values of zero correspond to the lowest 'risk' of denning relative to the remaining packs (i.e. poor predictive ability); whereas, values of one correspond to the highest 'risk' of denning (i.e. perfect predictive ability). Concordance is then estimated as the weighted average of these rankings across all denning events, with values approaching one indicative of stronger predictive accuracy.

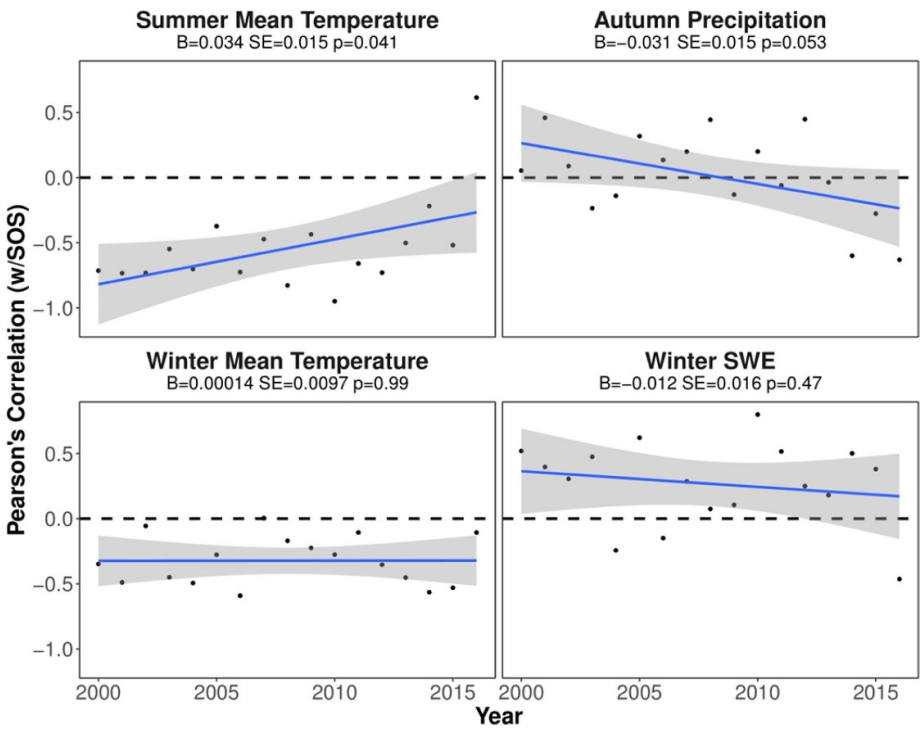


**Figure 4.** Panels showing the temporal trends in Pearson's correlation coefficients between start of growing season (SOS) and each local climate metric from the preceding season paired by study population. Each point estimate reflects a single pairwise correlation coefficient for all eight study populations in a given year. The purpose is to highlight the potential for preceding seasonal conditions to cue spring onset and may indicate to what extent species can depend on these metrics as indicators of future conditions.

## 3. Results

### 3.1. Denning summary

We compiled movement data from 388 wolves and identified 227 possible dens associated with 106 packs across western Canada and Alaska between 2000 and 2017. Of these, we classified reproductive success for 186 reproductive events in those packs with sufficient movement data (i.e. data from denning through the end of August and $\geqslant$1 fix per day). Although rare, we treated multiple litters as a single event based on the timing of the first den and any pup-rearing movements through August as a single measure of success. Validations comparing our movement-based predictions to aerial and ground observations of denning indicated that we successfully identified 100% of the known denning events ($n = 146$ known dens). We had two or more collared individuals for 41 of these dens, permitting us to calculate variation in estimated den date across individuals of different sex and breeding status. The median difference was 1 d ($\mu = 1.95$, SE = 0.31, range = 0 d to 8 d).

Of 153 confirmed aerial or ground observations of recruitment (i.e. packs with or without pups after August 31st of each year), 143 cases matched our predictions of success (93.5%). Of the ten misidentified, six were estimated as failures but observed to be successful and three were estimated as successful but observed to be failures. Thus, error in recruitment classification was relatively minor without, we believe, inducing any systematic bias associated with the 'type' of error due to near equal representation. We corrected the ten misidentified reproductive success estimates to reduce the overall classification error rate in our data set.

### 3.2. Inter-seasonal climate correlations: summer, autumn, winter correlations with SOS

Autumn and winter mean temperatures were negatively correlated with start of growing season (Autumn: $r_{\text{mean}} = -0.50$, SE = 0.07; Winter: $r_{\text{mean}} = -0.40$, SE = 0.05) and did not show a trend over the 18-year period for which we had data (2000–2017) (figure 4). Summer temperature was also negatively correlated with SOS ($r_{\text{mean}} = -0.57$, SE = 0.09) but demonstrated a slight trend toward weaker correlation in recent years. Summer and winter precipitation, as well as winter SWE, showed slight but highly variable correlations with SOS and no apparent temporal trend (figure 4). However, autumn precipitation exhibited a temporal trend, switching from positive to negative correlation during the same 18 year period.

### 3.3. Denning phenology

The estimated median denning date was May 4 (SD = 13.6 d), on average 14.7 d prior to the start of season. SOS advanced an average of 14.2 d from 2000 to 2017, whereas the median denning date did not change (figures 3(a) and S1 (available

online at stacks.iop.org/ERL/15/125001/mmedia)). Denning was initiated earlier at lower latitudes, but variability in the timing of denning occurred among all populations. Latitude was strongly correlated with seasonal temperatures (e.g. Winter $T_{max}$: $r = -0.77$), as was SOS and SDD ($r = 0.83$). Because effects of latitude and SDD were largely accounted for by the other climate variables (figure S2), latitude and SDD were removed from further consideration in this analysis. Further, we limit our discussion to seasonal maximum temperatures because of consistent model interpretations and generally improved model fit over minimum temperatures. Approximately 18.1% of phenology models expressed some degree of uninformative covariates (Leroux 2019). When present, these covariates consisted of LOS (5.5%), SOS (2.3%), autumn precipitation (4.3%), summer precipitation (3.7%), and autumn temperature (2.3%), which were consistent with relatively low parameter weights for these covariates (table 5). Models with evidence of uninformative covariates did not appear in our top models (table 4).

The best model ($\Delta$AICc relative to null $= -43.52$; Concordance $= 0.67$, SE $= 0.02$) for denning phenology included winter and summer maximum temperatures, tiNDVI, annual PDO, and autumn precipitation in order of support via parameter weights (tables 4 and 5). In general, denning occurred earlier in regions or years with warmer temperatures during summer and winter seasons preceding parturition. However, denning was delayed following years with higher tiNDVI and PDO, as well as with higher precipitation in autumn and winter (table 5).Importantly, our results may indicate that wolf reproductive phenology was responding to photoperiod, or latitude as a proxy, rather than winter temperatures (Asa and Valdespino 1998). Although statistically intractable due to a strong correlation between latitude and winter temperature, we included an additive effect of latitude within our best reproductive phenology model to evaluate how the two metrics were confounded. Notably, the model maintained significant effects for winter ($\beta = 0.25$; SE $= 0.13$) and summer temperatures ($\beta = 0.27$; SE $= 0.09$), but estimated a non-significant effect for latitude ($\beta = -0.20$; SE $= 0.15$). Though qualitative, this result would indicate there was some redundancy between temperature and latitude (i.e. photoperiod), but that seasonal temperatures were capturing additional variation independent of latitude; therefore, temperatures were more informative drivers of phenology at both regional and local population levels.

### 3.4. Reproductive success

The best model for reproductive success included autumn precipitation, summer maximum temperatures during pup-rearing, annual PDO, and home range area (in order of support via parameter weights) ($\Delta$AICc $= -15.85$ relative to the null model; $R^2 = 0.22$; table 5). Model-averaged coefficient estimates indicated pup recruitment through the end of August increased significantly with positive PDO during the previous year and declined with increased autumn precipitation, increased summer maximum temperatures during the current pup-rearing season, and increased home range area (tables 4 and 5; figure 5). We found no support for a linear effect, second-order polynomial, or a linear piecewise response to synchrony with spring onset (with a knot at perfect synchrony). The piecewise analysis allowed testing for differences in reproductive success whether animals denned early or late relative to the mean difference between den date and SOS. The confidence intervals for both piecewise coefficients overlapped 0 ($\beta_{<0} = -0.23$, $CI_{95} = -1.05$ to 0.59; $\beta_{>0} = 0.21$, $CI_{95} = -0.42$ to 0.84), indicating no difference in the influence of phenological match on reproductive success between cases where denning occurred early or late relative to SOS. Approximately 35.1% of success models expressed some degree of uninformative covariates (Leroux 2019). When present, these covariates consisted of annual AO (13.0%), autumn temperature (10.2%), winter temperature (5.4%), match with SOS (3.2%), summer precipitation (2.6%), and tiNDVI (0.7%), which were also consistent with relatively low parameter weights for these covariates (table 5). Models with uninformative covariates did not appear in our top models (table 4).

## 4. Discussion

Species' phenological responses to climate change have garnered significant research interest in recent years (Post and Forchhammer 2008, Aubry *et al* 2013, Thackeray *et al* 2016). Only a few of these studies have established a mechanistic link between demography and phenological match with optimal conditions and highlighted the costs to survival or reproductive success of being too early or too late (Rode *et al* 2018). Here, we identified a disconnect between climate factors signaling denning phenology from those that influenced reproductive success in gray wolves. Although warming temperatures have advanced spring start of growing season by approximately 2 weeks in less than two decades in our study region, both the timing and success of reproduction were insensitive to spring advancement despite sensitivity to seasonal conditions. These findings highlight that changes in the timing and magnitude of environmental conditions may each have distinct effects on species as climate change continues.

The gestation period of many mammals creates a temporal disconnect between breeding and offspring birthing seasons. Thus, climate cuing is likely most effective at signaling future climatic states (e.g. during parturition) in cases where such cues are strongly correlated with desirable environmental conditions

**Table 4.** Top models (ΔAICc < 2) for each of three analyses evaluating the effect of climatic signals on grey wolf denning phenology and reproductive success and the associated degrees of freedom (DF), the relative change in Akaike Information Criterion corrected for small samples sizes (ΔAICc), and goodness-of-fit (concordance for phenology and conditional pseudo-$R^2$ for success). Model weights are based on 2124 models in each analysis. Covariate names are described in detail within table 3.

| Denning phenology | | | | | | |
|---|---|---|---|---|---|---|
| Model | Model Coefficients | K | LL | ΔAICc | Weight | Concordance |
| 1 | Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO | 5 | −964.94 | 0.00 | 0.031 | 0.670 |
| 2 | Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO | 6 | −964.10 | 0.44 | 0.025 | 0.670 |
| 3 | tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO | 5 | −965.20 | 0.52 | 0.024 | 0.666 |
| 4 | Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX | 4 | −966.30 | 0.63 | 0.022 | 0.661 |
| 5 | tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO | 4 | −966.31 | 0.65 | 0.022 | 0.663 |
| 6 | Annual_AO + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO | 6 | −964.55 | 1.35 | 0.016 | 0.671 |
| 7 | Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO | 6 | −964.59 | 1.42 | 0.015 | 0.673 |
| 8 | Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO | 7 | −963.63 | 1.63 | 0.014 | 0.675 |
| 9 | Annual_AO + Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_TMAX | 5 | −965.77 | 1.66 | 0.013 | 0.666 |
| 10 | Annual_AO + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO | 5 | −965.81 | 1.75 | 0.013 | 0.667 |
| 11 | Autumn_PRCP + tiNDVI + Summer_PRCP + Summer_TMAX + Winter_TMAX + Annual_PDO | 6 | −964.78 | 1.80 | 0.012 | 0.669 |
| 12 | Autumn_PRCP + tiNDVI + Summer_TMAX + Winter_SWE + Winter_TMAX | 5 | −965.85 | 1.82 | 0.012 | 0.663 |
| 13 | tiNDVI + Summer_PRCP + Summer_TMAX + Winter_TMAX + Annual_PDO | 5 | −965.86 | 1.85 | 0.012 | 0.663 |
| 14 | Autumn_PRCP + Autumn_TMAX + tiNDVI + Summer_TMAX + Winter_TMAX + Annual_PDO | 6 | −964.82 | 1.89 | 0.012 | 0.669 |
| 15 | tiNDVI + Summer_PRCP + Summer_TMAX + Winter_SWE + Winter_TMAX + Annual_PDO | 6 | −964.87 | 1.97 | 0.011 | 0.665 |
| 16 | Null | 0 | −991.83 | 43.52 | 0.000 | 0.500 |
| Reproductive success | | | | | | |
| Model | Model coefficients | K | LL | ΔAICc | Weight | Cond. $R^2$ |
| 17 | HR_Area + Autumn_PRCP + Summer_TMAX* + Annual_PDO | 7 | −94.02 | 0.00 | 0.036 | 0.216 |
| 18 | HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_SWE + Annual_PDO | 8 | −93.22 | 0.58 | 0.027 | 0.243 |
| 19 | HR_Area + Autumn_PRCP + tiNDVI + Summer_TMAX* + Annual_PDO | 8 | −93.31 | 0.75 | 0.025 | 0.224 |
| 20 | HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_TMAX + Annual_PDO | 8 | −93.35 | 0.85 | 0.023 | 0.236 |
| 21 | HR_Area + Autumn_PRCP + Summer_TMAX* + Winter_SWE + Winter_TMAX + Annual_PDO | 9 | −92.42 | 1.20 | 0.020 | 0.265 |
| 22 | HR_Area + Autumn_PRCP + tiNDVI + Summer_TMAX* + Winter_SWE + Annual_PDO | 9 | −92.49 | 1.33 | 0.018 | 0.248 |
| 23 | HR_Area + Autumn_PRCP + tiNDVI* + Summer_TMAX* + Annual_PDO | 8 | −93.76 | 1.66 | 0.016 | 0.213 |
| 24 | HR_Area + Autumn_PRCP + tiNDVI* + Summer_TMAX* + Winter_SWE + Annual_PDO | 9 | −92.70 | 1.75 | 0.015 | 0.245 |
| 25 | Null | 3 | −106.20 | 15.85 | 0.000 | 0.089 |

at the time of the phenological event. Understanding how correlated, and therefore effective, these cues are through time can provide important insights into how climate change might be expected to influence species phenology. Here, given the adherence to spring parturition in wolves, we found that winter

**Table 5.** The parameter weights, model-averaged estimates, and confidence intervals (L85: lower 85% confidence limit, U85: upper 85% confidence limit) for each coefficient considered within three distinct analyses evaluating the effect of climatic signals on grey wolf denning phenology and reproductive success. Coefficient and confidence interval estimates were derived from standardized covariates and unconditional standard errors, respectively. As time-to-event models, negative coefficients indicate later denning and vice versa.

| Coefficient | Parameter weight | Estimate | L85 | U85 |
|---|---|---|---|---|
| *Denning phenology* | | | | |
| Winter_TMAX | 1.00 | 0.34 | 0.20 | 0.48 |
| Summer_TMAX | 0.98 | 0.30 | 0.16 | 0.45 |
| tiNDVI | 0.94 | −0.32 | −0.47 | −0.17 |
| Annual_PDO | 0.64 | −0.14 | −0.26 | −0.03 |
| Fall_PRCP | 0.57 | −0.14 | −0.27 | −0.01 |
| Winter_SWE | 0.46 | −0.10 | −0.21 | 0.01 |
| Annual_AO | 0.38 | −0.08 | −0.18 | 0.03 |
| SOS[a] | 0.32 | 0.10 | −0.16 | 0.35 |
| Summer_PRCP | 0.30 | 0.04 | −0.11 | 0.19 |
| Fall_TMAX | 0.28 | 0.05 | −0.11 | 0.20 |
| LOS | 0.28 | 0.01 | −0.20 | 0.22 |
| *Reproductive success* | | | | |
| Fall_PRCP | 0.90 | −0.61 | −0.96 | −0.27 |
| Summer_TMAX[b] | 0.88 | −0.68 | −1.05 | −0.32 |
| Annual_PDO | 0.75 | 0.49 | 0.18 | 0.80 |
| HR_Area | 0.70 | −0.54 | −0.93 | −0.16 |
| Winter_SWE | 0.35 | −0.26 | −0.54 | 0.02 |
| Winter_TMAX | 0.32 | 0.30 | −0.07 | 0.67 |
| tiNDVI | 0.30 | −0.34 | −0.71 | 0.03 |
| Summer_PRCP[b] | 0.24 | 0.23 | −0.21 | 0.68 |
| Den match with SOS | 0.24 | 0.20 | −0.16 | 0.57 |
| tiNDVI[b] | 0.19 | −0.24 | −0.59 | 0.12 |
| Fall_TMAX | 0.18 | −0.03 | −0.37 | 0.30 |
| Annual_AO | 0.17 | −0.02 | −0.31 | 0.27 |

[a]Measured the previous year

[b]Measured the summer after denning.

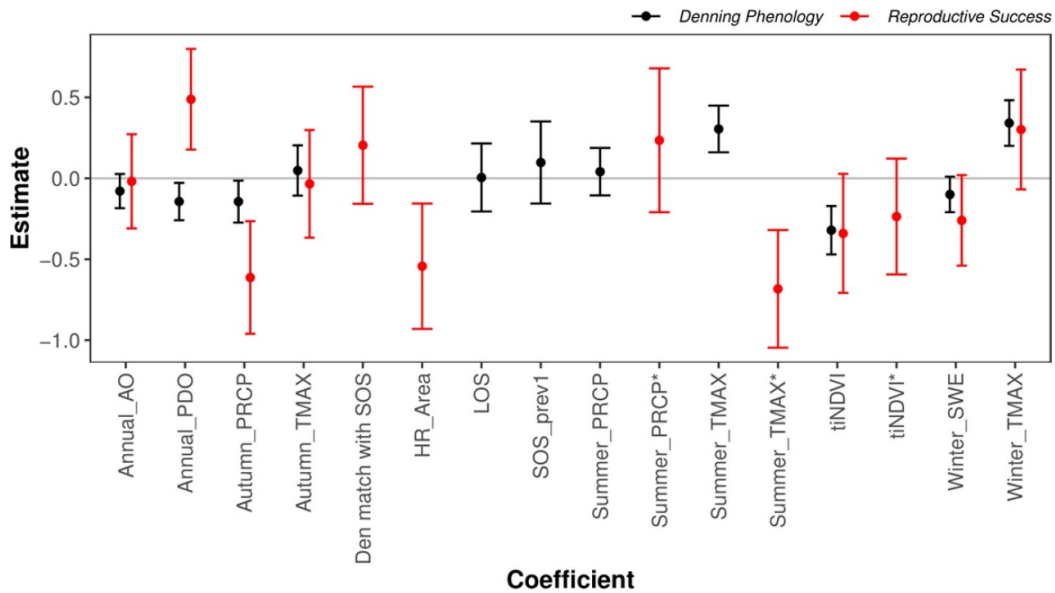


**Figure 5.** Coefficient plots for all model averaged coefficients in an assessment of gray wolf denning phenology (black; Cox proportional hazard regression) and reproductive success (red; generalized linear mixed model). Coefficients with a '*' indicate covariate measurements that were made during the denning period. All remaining coefficients were derived from measurements made during seasons preceding the denning period. Error bars represent 85% confidence intervals derived from unconditional standard errors.

temperature was the best and most consistent predictor of both spring onset and denning phenology, with the lowest interannual variability and no temporal trend in correlation strength during the 18 year

study period. However, previous summer temperature was also a strong predictor of wolf denning phenology, but may be a less reliable indicator of spring onset due to declines in correlation in recent years. These differences in the reliability of climate signaling highlight the importance of understanding which cues plant or animal populations may be using to time key life history events, and may be an underappreciated factor explaining variable responses among species to climate change.

As with many temperate carnivores, wolves exhibit a high degree of synchrony and seasonal fidelity in parturition phenology. Such seasonal birth cycles are likely indicative of climate-driven, temporal patterns in resource availability (Oftedal and Gittleman 1989), defined broadly as the abiotic conditions conducive to neonate survival (Russell *et al* 2002), the availability of materials needed for reproduction (e.g. den construction; Liston *et al* 2016, Rode *et al* 2018), or food for reproducing females and/or developing young (Regehr *et al* 2007, Inman *et al* 2012, Stirling and Derocher 2012). We found that wolf denning phenology was most responsive to local climate cues during the winter breeding season, with cooler winters delaying spring denning and parturition. Although winter temperature was an important predictor of denning phenology, wolves within our region did not respond to year-to-year variation in the start of growing season (orSDD), nor was their reproductive success sensitive to synchrony with spring onset. In addition, spring onset advanced approximately 14 d during the period from 2000 to 2017 across all populations. Although trends in SOS vary considerably at high latitudes and throughout the Arctic (e.g. 5.3 d decade$^{-1}$ to − 18.9 d decade$^{-1}$; Zeng *et al* 2013), our estimated rate of SOS advancement are in-line with those reported for other regions of the Arctic during a similar time period using remote sensing (e.g. 4.5 d decade$^{-1}$ to 5.1 d decade$^{-1}$ in Alaska's National Parks; Swanson 2017) and from ground observations (e.g. Greenland: 10 d from 2000 to 2013; Westergaard-Nielsen *et al* 2017). Yet, there was no statistical change in mean denning date across all populations over the same period (similar to Joly *et al* 2018). These patterns suggest that variation in the availability of spring denning habitat as defined by climatic suitability is not a limiting factor for wolves. Given the reproductive synchrony and adherence to spring denning within wolf populations, however, such insensitivity to interannual variation in spring onset may indicate wolves are responding to spring conditions at coarser temporal and spatial scales.

Indeed, the importance of PDO, a regional climate index, was evident in both denning phenology and success, suggesting wolf reproductive ecology is broadly responsive to regional climate patterns at time scales longer than a year. We chose PDO as a predictor because of its strong influence in the Arctic-boreal region of western North America, and large ungulate population dynamics specifically (Post and Forchhammer 2002, Hebblewhite 2005, Hegel *et al* 2010a). For our populations, positive annual PDO was associated with warmer winters, earlier start of growing season, and reduced winter precipitation in those populations experiencing the deepest snowfalls (figure S3). Our results indicated regional warm and dry cycles (i.e. larger PDO) delayed timing of denning the following year (notably, CIs indicated non-significance by 0.01), opposite of both temperature and precipitation effects at local levels. Wolf parturition could be delayed in response to increases in prey populations that often occur during positive PDO cycles (Hebblewhite 2005, Hegel *et al* 2010a, Joly *et al* 2011) because higher densities may reduce maternal body condition, increase gestation length, and lead to delayed parturition in many of the ungulate species that wolves prey upon in the region (Cameron *et al* 1993, Singer *et al* 1997, Keech *et al* 2000). Reproductive phenology of large carnivores should correspond to prey phenology, whether peak parturition or timing of migration (Klaczek *et al* 2015), and the extent to which wolves respond to climatic conditions may depend upon the scale and magnitude of a climate response in their prey base. Although we did not test the relationship here, it is also possible that variation in wolf phenology may be sensitive to both the diversity of available prey species and the temporal changes in their availability.

Climatic drivers that affect kill rates during parturition for large carnivores, such as the availability and vulnerability of ungulates or the availability of alternative prey during the summer (e.g. fossorial mammals and Canadian beaver, *Castor canadensis*), may also be important to reproductive success (Messier 1994, Vucetich *et al* 2002, Frame *et al* 2008). Our results indicated that increased autumn precipitation decreased the odds of pup recruitment the following summer. Higher than average precipitation from late autumn through early spring, particularly in the form of snow, can contribute to reduced overwinter survival in many large ungulates, disproportionately affecting the most vulnerable age classes (White *et al* 2011, Van de Kerk *et al* 2018). Although this may provide a short-term benefit to carnivores in terms of elevated prey vulnerability during winter (Hebblewhite 2005, Carroll 2007, Metz *et al* 2012), particularly harsh over-winter conditions may precipitate sharp population declines in both ungulate (Blackburn and Duncan 2001, Ims *et al* 2008, Vors and Boyce 2009, Hegel *et al* 2010a, Albon *et al* 2017) and non-ungulate prey (Morrison and Hik 2007, Patil *et al* 2013) the following summer, thereby reducing prey availability during the wolf pup-rearing period. The large, positive effect of PDO, for which positive cycles are commonly associated with larger northern ungulate populations (Hebblewhite 2005, Hegel *et al* 2010a, 2010b, Joly *et al* 2011), and irruptions in

rodent populations (Morrison and Hik 2007) which can serve as supplementary prey for wolves (Latham *et al* 2013, Gable *et al* 2018), provides further support for the possible role of prey abundance in determining reproductive success (White 2008). Similarly, as 'central-place' foragers during a period when young are stashed at pup-rearing sites and are relatively sedentary (Mills and Knowlton 1991, Frame *et al* 2008), we found that home range area during pup-rearing was negatively correlated with reproductive success, indicating wolf packs that needed to travel more during the summer months, presumably in search of food, were less successful. Of the remaining summer covariates, we found moderate support for reduced wolf reproductive success during hotter summers. As coursing predators during a period of the year with extended daylight, higher temperatures may reduce time spent hunting due to increased physiological stress akin to what has been observed in African wild dogs (*Lycaon pictus*; Woodroffe *et al* 2017). Although our results establish a clear link between climate and wolf reproductive ecology, we could not directly test these relationships due to lack of sympatric data on prey dynamics during our study period. A multi-trophic analysis of responses to climate variability would be a valuable next step to reveal mechanisms by which climate-induced phenological shifts impact higher trophic levels.

## 5. Conclusions

Climate change is increasingly recognized as one of the major causes of species endangerment (Stanton *et al* 2015). Local and regional changes in climate have altered the phenology and distribution of plant and animal species across a range of ecosystems (Parmesan 2006). Range shifts (or contractions) and phenological advancements coincident with observed climate trends have occurred disproportionately across species within communities (Parmesan and Yohe 2003), contributing to the destabilization of species interactions including those between predators and prey (Parmesan 2006, Ripple *et al* 2014). Although there is a growing body of literature that suggests large carnivores may buffer communities and ecosystems against the detrimental effects of climate change (Wilmers and Getz 2005, Gormezano and Rockwell 2013, Ripple *et al* 2014), few studies have investigated the direct impact of climate on large carnivore demography across a large geographic domain. Our results indicated that climate can interact with carnivore reproduction in complex and nuanced ways. We found no evidence indicating that advancing spring onset, nor the ability of individuals to synchronize denning with spring onset, was detrimental to wolf reproductive success, at least within the range of observed changes in climate. Although this would indicate carnivores are likely quite resilient to shifts in seasonality, we also found wolf reproductive success was sensitive to weather conditions that likely shaped the availability, vulnerability, and hunting success of large ungulates. Thus, carnivore persistence may depend on the ability of prey species to respond adaptively to weather conditions at local or regional scales and avoid destabilizing predator-prey dynamics (Stenseth and Mysterud 2002, Visser *et al* 2004, Durant *et al* 2007). Future efforts to evaluate carnivore phenological response to climate signals would benefit from explicit consideration of the differential responses of predator and prey to climate dynamics. Doing so will help elucidate carnivore resilience under continued climate change as well as provide clarity on whether predators can serve as 'climate buffers' within communities through population regulation (Wilmers *et al* 2012).

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## Conflict of interest

All authors declare that there are no conflicts of interest in the publication of our findings.

## Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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