OXFORD

## Article

# Reconstructing landscapes of ungulate parturition and predation using vegetation phenology

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*Handling editor: Yan-Ping Wang*

## Abstract

Enhanced vegetation index (EVI) data can be used to identify and define the space in which ungulates practice parturition and encounter predation. This study explores the use of EVI data to identify landscapes linked to ungulate parturition and predation events across space, time, and environmental conditions. As a case study, we used the moose population (*Alces alces*) of northern Minnesota in the USA. Using remotely sensed EVI data rasters and global positioning system collar data, we quantified how vegetation phenology and moose movement shaped the births and predation of 52 moose calves from 2013 to 2020 on or adjacent to the Grand Portage Indian Reservation. The known sources of predation were American black bears (*Ursus americanus*, $n = 22$) and gray wolves (*Canis lupus*, $n = 28$). Satellite-derived data summarizing seasonal landscape features at the local level revealed that landscape heterogeneity use by moose can help to quantitatively identify landscapes of parturition and predation in space and time across large areas. Vegetation phenology proved to be differentiable between adult moose ranges, sites of cow parturition, and sites of calf predation. Landscape characteristics of each moose group were consistent and tractable based on environment, suggesting that sites of parturition and predation of moose are predictable in space and time. It is possible that moose selected specific landscapes for parturition despite risk of increased predation of their calves, which could be an example of an "ecological trap." This analytical framework can be employed to identify areas for future ungulate research on the impacts of landscape on parturition and predation dynamics.

Key words: bear, EVI, moose, parturition, predation, prey, vegetation phenology.

Phenology, the study of cycling natural phenomena, aims to understand how landscape and seasonality impact the movement and interactions of species. One such avenue of study includes the ever-cycling events of parturition (births) and predation (deaths) within predator–prey animal systems. Landscape variables and seasonality have been shown to influence both prey movement across heterogeneous landscapes and predation (Kauffman et al. 2007; Leblond et al. 2010; Whittington et al. 2011; Latham et al. 2013; Turner and Gardner 2015). Previous studies have assessed how landscape heterogeneity affects predation, and have noted that behavioral modification of prey is reliant upon the costs and benefits of anti-predator behavior (Kauffman et al. 2007; Schmitz et al.

2010; Beschta and Ripple 2013). Specifically, vegetative characteristics related to food and cover availability can play into these energetic tradeoffs (Kauffman et al. 2007; Leblond et al. 2010). Predator avoidance strategies in general have energetic costs that can outweigh risks of predation (Kauffman et al. 2007; Creel 2011; Stears and Shrader 2015). For example, ungulates have been shown to change their land use patterns and increase their risk-taking behavior to access higher-quality food (Creel et al. 2005; Stears and Shrader 2015). The inverse has also been observed, where ungulates avoid high-quality forage to mitigate predation risk (Tadesse and Kotler 2012; Bleicher and Rosenzweig 2018). Furthermore, individual-level factors, such as pregnancy stage, have been shown to modulate predation risk in ungulates, as individuals will begin using low-quality food to reduce risk during late stages of the pregnancy, before parturition (Berger 1991). Female ungulates have also been shown to heavily alter their movement during seasons of parturition (Ciuti et al. 2006; Bongi et al. 2008; Long et al. 2009; Mcgraw et al. 2014; Severud et al. 2015, 2019). Little research exists, however, regarding phenology investigations that account for the effects of landscape variation on predation risk and parturition in the biological life cycle of ungulates. It is therefore important for researchers and managers to understand how landscape seasonality impacts the physical areas where parturition and predation overlap.

Different aspects of landscape function and structure can be reliably monitored via the spectral signatures of vegetation captured remotely (e.g., satellite imagery; Huete et al. 2002; Turner et al. 2003; Horning et al. 2010; Turner and Gardner 2015). One such example of satellite-derived vegetation phenology is the vegetative metric referred to as the enhanced vegetation index (EVI; Huete et al. 2002; Villamuelas et al. 2016). EVI data are functional because chlorophyll from photosynthetically active vegetation absorbs light in red wavelengths of the optical spectra, whereas mesophyll scatters light in near-infrared wavelengths (Huete et al. 2002). By observing these spectral variations captured by the satellite, EVI and other vegetation indices can be used to identify, quantify, and monitor vegetation canopy greenness and structure across time and space (Waring et al. 2006; Yang et al. 2017).

EVI data provide positive and strong relationships with primary productivity and, because EVI reduces effects of radiometric contaminants from the atmosphere, it is an improved version of the normalized difference vegetation index (Horning et al. 2010). EVI can also functionally act as a surrogate representative for growing degree days, soil characteristics, humidity, and temperature (Waring et al. 2006; Hassan 2007), and as such this metric can reasonably act as a unifying environmental variable. EVI has also been shown to function as a good assessment for ground vegetation dynamics, plant phenology, canopy structure, and as a proxy for diet composition and quality for ungulates (Hassan 2007; Villamuelas et al. 2016). Furthermore, EVI correlates with changes in land elevation and aspect, and is more sensitive to topographic effects, such as variations in radiance due to changes in surface slope and aspect of the terrain (Matsushita et al. 2007). EVI data have also been used to quantify the spatial distribution of vegetation in dynamic landscapes (Matsushita et al. 2007; Mokarram and Sathyamoorthy 2015; Moreira et al. 2016). EVI can therefore be used to describe landscape heterogeneity due to its correlation with environmental and topographic features within diverse landscapes (Matsushita et al. 2007).

Recent phenology studies have revealed that ungulate parturition and post parturition movement is associated with specific seasons and landscapes that have denser cover (e.g., lowland conifer shrub lands and deciduous forests) (Mcgraw et al. 2012, 2014; Severud et al. 2015). Related to this movement, patterns of predation by large predators can vary among seasons due to related changes in prey vulnerability (Metz et al. 2012). Parturition has also been shown to follow patterns of vegetation primary productivity across the growing season (Stoner et al. 2016). In a relative cycle, it therefore tracks that vegetation phenology has impacts on the sites and seasons of ungulate parturition, and as a result, also impacts the timing and location of predation.

Our study question was: what is the extent to which vegetation phenology can be used to reconstruct when and where ungulate parturition and subsequent calf predation occurs? We hypothesized that EVI data collected from across time and space can be used to reconstruct and predict specific landscapes where parturition and predation are likely to occur. We also predict that ungulate parturition and subsequent calf predation will be associated with higher levels of primary productivity and with early peak or peak seasons of greenness (i.e., higher values of EVI), making the site and time of ungulate parturition and predation predictable using EVI data.

## Materials and Methods

### Case study system
As a case study, we used the predator–prey system of moose *Alces alces*, grey wolves *Canis lupus*, and American black bears *Ursus americanus* on and near the Grand Portage Indian Reservation in Minnesota, northern USA. We chose this system because moose inherently have a wide ecological impact, both as a large herbivore and as a prey species for many keystone predators (Sneft et al. 1987; Miller and Ballard 1992; Persson et al. 2000; Ditmer et al. 2018; Mech et al. 2018). Moose are also a subsistence species for many Native American tribes, where they have been harvested by these communities for survival for centuries (Kuhnlein and Humphries 2017), making this species one of conservation concern. Furthermore, the northeastern moose population in Minnesota has experienced a decline in recent history due to low calf recruitment (Lenarz et al. 2009, 2010). Therefore, understanding where and when moose calves are killed by predators in this system could have cultural and conservation implications. Moose have also been the focus of a plethora of studies on various topics in ecology, specifically with regard to predator–prey relationships (Nicholson et al. 2014; Abom and Schwarzkopf 2016; Mech et al. 2018; Gaynor et al. 2019; Wierzchowski et al. 2019). This moose population in particular has been studied extensively and has sufficient historical data upon which our assessment could be conducted without risks of data deficiency (Wolf et al. 2021). As such this predator–prey relationship is well documented with regard to locational data on both parturition and predation of moose calves, and thereby represents a sufficient system in which to assess how EVI can be used to identify landscape impacts on sites of parturition and predation.

### Physiological and movement data collection
Data for this study originated from an ongoing long-term moose mortality project conducted by the Grand Portage Band of Chippewa (IACUC protocols 1410-31945A and 1803-35736A). Sampling was conducted in and around the Grand Portage Indian Reservation located in northeastern Minnesota, in Cook County (Supplementary Figure S1). Grand Portage shares its northern border with Ontario, Canada and adjoins a mixture of federal, state, and privately owned lands to the west, and Lake Superior to the

southeast. The reservation encompasses ~192 km² and is comprised of mostly coniferous forest (Minnesota Department of Natural Resources 2019). We first collected location data between February 2013 and May 2020 from collared adult female moose with offspring ($n = 140$). Moose cows were immobilized by helicopter darting of either thiafentanil oxalate (A3080), etorphine hydrochloride, or carfentanil citrate (Wildlife Pharmaceuticals, Inc., Windsor, CO USA) in combination with xylazine, which were reversed with naltrexone and tolazoline, respectively, as described previously (Wolf et al. 2021). Captured cows were fitted with global positioning system (GPS) Plus Iridium collars (Vectronic Aerospace GmbH, Berlin, Germany), equipped with a GPS data-logger that included a movement sensor and mortality signal, communicating a mortality event via satellite transmission when movement diminished below a programmed threshold after a period of six hours.

Cows were examined by rectal palpation for pregnancy and a subset was implanted with a vaginal implant transmitter (VIT; Vectronic Aerospace GmbH) near the cervix in the vaginal canal using a sterile, disposable vaginal speculum (Jorgensen Laboratories, Inc., Loveland, CO), as previously described (Johnson et al. 2006; Murray et al. 2012; Patterson et al. 2013; Wolf et al. 2021). This type of transmitter continuously measures body temperature and motion, transmitting data to the GPS collar at regular intervals. Cow movement was monitored via GPS satellite transmission, which involved daily assessments during the calving season. Parturition was signaled upon reduced temperature and cessation of motion of the VIT following expulsion during calving. We used VIT's in all cows captured in a given year ($n = 32$ per year); however, there were some cows that were collared in previous years and thus did not receive a VIT. The VITs enabled us to confirm that the movements we saw remotely were indeed parturition events, both for the VIT implanted cows, but those same movement patterns were consistent in nonimplanted cows as well. In cows that were collared in previous years, where a VIT was not present, parturition was recognized by a significant increase in movement characterized by an abrupt geographical localization that remained constant over several days or weeks as reported elsewhere (Mcgraw et al. 2014). The use of these two methods allowed for increased accuracy in the detection of parturition.

We increased the GPS data collection frequency of cow collars from April to June each year from two hours to 30 minutes intervals to enhance observation of movement behaviors associated with parturition. Approximately 48–72 hours after parturition was signaled cows were located and the calves captured and collared, as described by Wolf et al. (2021). This time frame was chosen to allow maximum cow-calf bonding, based on previous evidence that some capture-induced abandonment by the cows may result from calf handling prior to sufficient bonding (Ballard et al. 1979, 1991; Patterson et al. 2013). Over the time frame of 2013–2020, we observed seven abandonment events from 44 calf-collaring events and the 140 calves investigated. A two or three person capture crew approached the cow-calf pair rapidly on foot to induce a flight response from the cow for calf handling. Calves were blindfolded and manually restrained in sternal recumbency for data collection. A GPS Globalstar collar was placed (Vectronic Aerospace GmbH), designed with an expandable, elastic band to increase in diameter as calves grew and break away within one year. Collars were equipped with the same movement sensor and mortality signaling mechanism as adult GPS collars. Calf processing occurred over a mean duration of 5.7 minutes (SD ± 4.81 minutes). Collared calves were subsequently monitored daily by GPS until mortality signaling, at which time the collar location was investigated.

Additional cows with noncollared calves were monitored remotely for calving and predation using cow GPS movement data (Severud et al. 2019; Wolf et al. 2021). Specifically, we monitored cow GPS data for changes in movement characterized by tight localization of GPS data points following longer movement patterns, indicative of parturition or, following parturition, long-distance movements within a short time frame from a central focus of GPS data points, suggestive of a predation event. We monitored and investigated predation events of non-collared calves intensively for up to four weeks after parturition. Following this window, it became increasingly difficult to confirm mortality and predation without a collar-associated mortality signal due to increasing mobility of the calf with age. In cases where an intact carcass was recovered, it was submitted to the Minnesota Veterinary Diagnostic Laboratory (St Paul, MN) for post-mortem examination, histopathology, and, at the discretion of the pathologist, bacteriological, and/or virological screening. Cause of death was based on (1) comprehensive site investigation (particularly in cases of predation), (2) necropsy/histopathological examination, or (3) a combination thereof. Predator type was determined by the evidence left from the predation. For example wolf predations were classified as such based on scant calf remains, wolf scat, and hairs collected at the predation location. Black bear predations were characterized by remnants of intact skin, head, and legs of the calf, as well as bear scat at the predation location. Bears also occasionally cached whole-carcass remains, whereas wolves always consumed the entire calf. Predator hairs collected at predation locations were identified by microscopic morphologic analysis to determine hair scale patterns (Adorjan and Kolensoky 1969).

Geolocation of individuals was explored in terms of their temporal, geographic, and environmental distribution. More specifically, we identified the area used by adult and juvenile moose, location of parturitions, and location of mortality, the date of the events, and their environmental conditions in terms of EVI. To reduce spatial autocorrelation among the GPS data, we resampled coordinates to one per pixel of the study extent (250 m resolution). Thus only one location of each event (adult moose occurrence, parturition, or predation) was retained for each pixel (250 m). Resampling was done by converting each set of occurrence coordinates (i.e., locations of adult movement, parturition, or predation) into rasters in R statistical software with the same spatial resolution, then re-converting the resulting reduced set of coordinates (one occurrence per pixel) to a data frame (R Core Team 2019). This filtering mitigated the risk of autocorrelation and over-representation of some environmental conditions.

## Remote sensing data collection

To reconstruct the environmental conditions in the study area, we used a set of EVI rasters from the Moderate Resolution Imaging Spectroradiometer sensor onboard the National Aeronautics and Space Administration's Terra satellite, generated every 16 days at 250-m spatial resolution and available at the Land Processes Distributed Active Archive Center (LP DAAC; LP DAAC 2019). EVI rasters were collected for the study period in HDF - EOS (Hierarchical Data Format - Earth Observing System) file format in Sinusoidal projection and converted to GeoTiff in WGS84 geographic projection restricted to the Grand Portage Indian Reservation area (latitude 47.30° N, 48.31° N longitude 90.50° W, 88.99° W). Rasters were then combined to generate monthly

averages for EVI value, which was done to reduce spectral gaps often caused by cloud cover (Poggio et al. 2012). Monthly averages were then used for all analyses.

### Data analyses

A principal component analysis was developed from the original EVI dataset to reduce the dimensionality and correlation among rasters. Each raster, therefore, acts as a temporal and environmental parameter from which "loads," (i.e., loadings) of each principal component could be ascertained. A loading table was also made to assess how each raster correlated to each retained principal component (Swan and Sandilands 1995; Legendre and Legendre 1998; Borcard and Legendre 2002; Borcard et al. 2011; Supplementary Table S1). The first three components were retained and used as vector axes to summarize major landscape patterns in Niche Analyst (NicheA) software (Qiao et al. 2016). NicheA allows users to visualize species or event occurrences in a 3-D space built from vectors of environmental data (Qiao et al. 2016). These vector axes could be, for example, unique climatic or environmental variables such as precipitation, soil composition, or temperature, or they could be principal components axes. The 3-D "environmental space" created between these vectors represents the environmental conditions of the landscape as measured by the selected environmental variable or variables. Species or event occurrences can then be plotted by environment (i.e., in environmental space), rather than just by latitude or longitude (i.e., in geographic space). Using a convex polyhedron approach, we determined the size, position, and shape of the multivariate space used by adult cows, areas of parturition, and areas of calf mortality to determine whether areas of parturition and predation occurred across the bulk of the environment, or whether parturitions and predations occurred under specific environmental conditions in terms of EVI. That is, we assessed the conditions where biotic interactions occurred against the conditions used by moose. These polyhedrons were then used to quantified landscape similarity in terms of polyhedron volume overlap within NicheA from sites with adult moose, parturition, and predation (Qiao et al. 2016). A visual representation of this workflow can be found in Supplementary Figure S2.

We assessed the polyhedrons from parturition and predation landscapes to predict predation using a cumulative binomial probability test accounting for the total number of predation events (i.e., trials), percentage of predation events predicted correctly (i.e., observed success), and proportion of area predicted from the total study area (i.e., of success probability; Peterson 2012). Landscape similarity based on multidimensional overlaps was quantified using the Jaccard Similarity index and the Sørensen–Dice index. Both indexes are used to measure the similarity of two sets of data, and quantify differentiation via index similarity with a range from zero to one (i.e., the lower the index value the more dissimilar the landscape conditions; Jaccard 1912; Dice 1945; Levandowsky and Winter 1971; Moulton and Jiang 2018). EVI values from each 16-day raster within the study period (February 2013 to May 2020) were then averaged by month to compose an average representation of the annual growing season within the study area to EVI values for sites with adult moose, parturition, and predation.

## Results

We obtained a total of 140 sites of cow parturition and 52 of calf predation over the course of this study (February 2013 to May 2020). We note that sites of parturition that involved twins were counted as a singular parturition event to avoid over counting. The same was done for sites of predation. We confirmed 28 calf predation sites linked to wolves, 22 linked to bears, and two of unknown predator origin (Figure 1C). Resampled occurrences of adult moose resulted in 7,860 single locations. The principal components one (58.9%), two (16.3%), and three (2.1%) summarized 77.3% of the overall variance of the landscape data. Loadings for each of the first three principal components indicated that each monthly EVI raster had both negative and positive correlations with each principal component (Supplementary Table S1). The landscape heterogeneity (i.e., difference in EVI values across the geographic space) was visualized with different colors representing each principal component (Figure 1A), showing the elaborate pattern of variability across the landscape.

Both geographic mapping and environmental space visualization of the distribution of adult moose movement, parturition, and predation across environmental space revealed that moose are not utilizing the entire landscape conditions available to them. Adult moose used 70.54% of the entire suitable area available to them geographically (Figure 1C), but only 1.78% of that landscape was used for parturition (Figure 1C). When plotted in 3-D environmental space (i.e., by using monthly EVI principal components), parturition occurred in a specific sub-portion of the range of available landscapes used by adult moose (Figure 2A). Only 9.51% of the area used by adult moose was used for parturition. Similarity assessments in environmental space showed that landscapes of adult movement and sites of parturition had low similarity values (Jaccard similarity = 0.08, Sørensen–Dice index = 0.15; Figure 2B). Landscapes where parturition and predation occurred, however, had higher similarity (Jaccard similarity = 0.36, Sørensen–Dice index = 0.53) (Figure 2C). Predation occurred almost exclusively in landscape conditions nested within landscapes of parturition, with predation occupying 86% of the area of parturition in environmental space (Figure 2D). The cumulative binomial probability test revealed polyhedrons containing parturition data predicted predation events better than by random expectation ($P < 0.05$). These results denote a significant correlation between sites of parturition and sites of predation.

Temporally, parturitions occurred between April and June annually, and the majority (94.13%) of predation events ($n = 50$) occurred in May and June, with the exception of two mortalities caused by wolves which occurred in November and December of 2013 and 2015, respectively (Supplementary Figure S3). Vegetation phenology in the study area revealed peaks of greenness each year in the months of May and June (Figure 3). Calf parturition occurred within expected timelines in relation to season and vegetation availability (April to June), and predation occurred shortly thereafter (May to July) (Figure 3; Supplementary Figure S3). Predation events were primarily evident through the beginning and peak (May to July) of the growing season among years (Figure 3). The landscape conditions of the 7-year time series revealed that sites of wolf predation have higher average EVI values (EVI mean = 3305.12, *Standard Deviation* = 1,588.60) compared with localities of bear predation (EVI mean = 2895.25, *Standard Deviation* = 1458.58) revealing significant peaks in May ($t_{2669} = 7.46$, $P = 0.001$) (Figure 3).

## Discussion

Our analyses have shown that adult moose are selective in their landscape usage, and EVI conditions clearly identified these habits (Figure 2). The EVI conditions of the adult movement (i.e., the
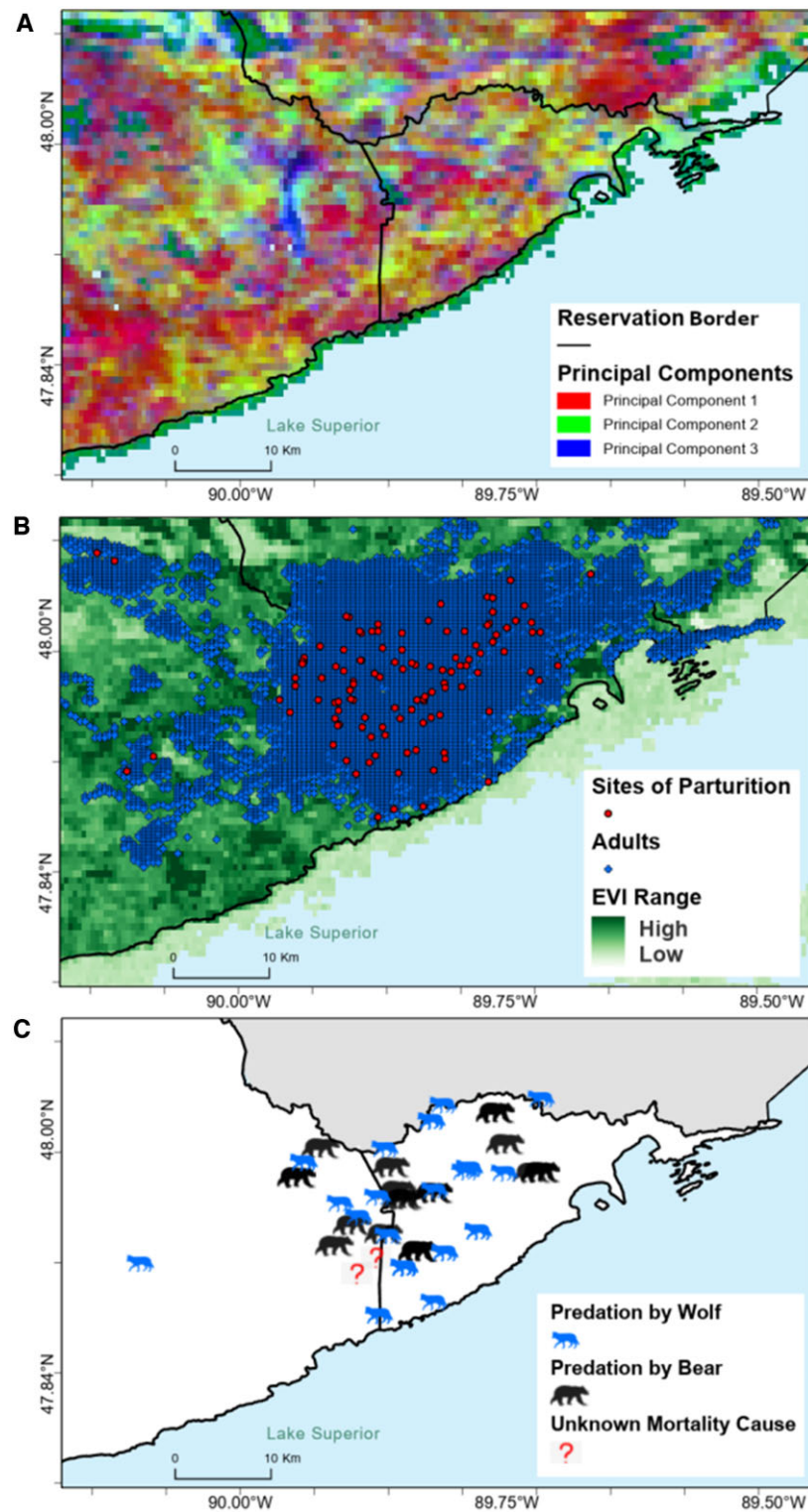
**Figure 1.** Landscape information in the study area. (**A**) Map of the study area showing landscape heterogeneity. Landscape heterogeneity is shown by the first three principal components from the principal component analysis of monthly EVI rasters. Colors represent the distribution of each principal component one (red), two (green), and three (blue) across the landscape. Heterogeneous landscape conditions were present across the study area, and are displayed as changes in color intensity and combination. (**B**) Distribution of adult moose (blue crosses) and sites of parturition (red points) resampled to one report per pixel (see Materials and Methods section). Adult moose reports cover a large geographic area within the study area. Monthly average EVI values are displayed in the background, ranging from high (dark green) to low (light green), to represent seasonal variation in primary productivity (i.e., EVI value) during the year. (**C**) Sites of calf predation by bears (black silhouettes), wolves (blue silhouettes), and sites of unknown calf mortality cause (red question marks). There was a dispersed distribution and overlap in sites of attacks.
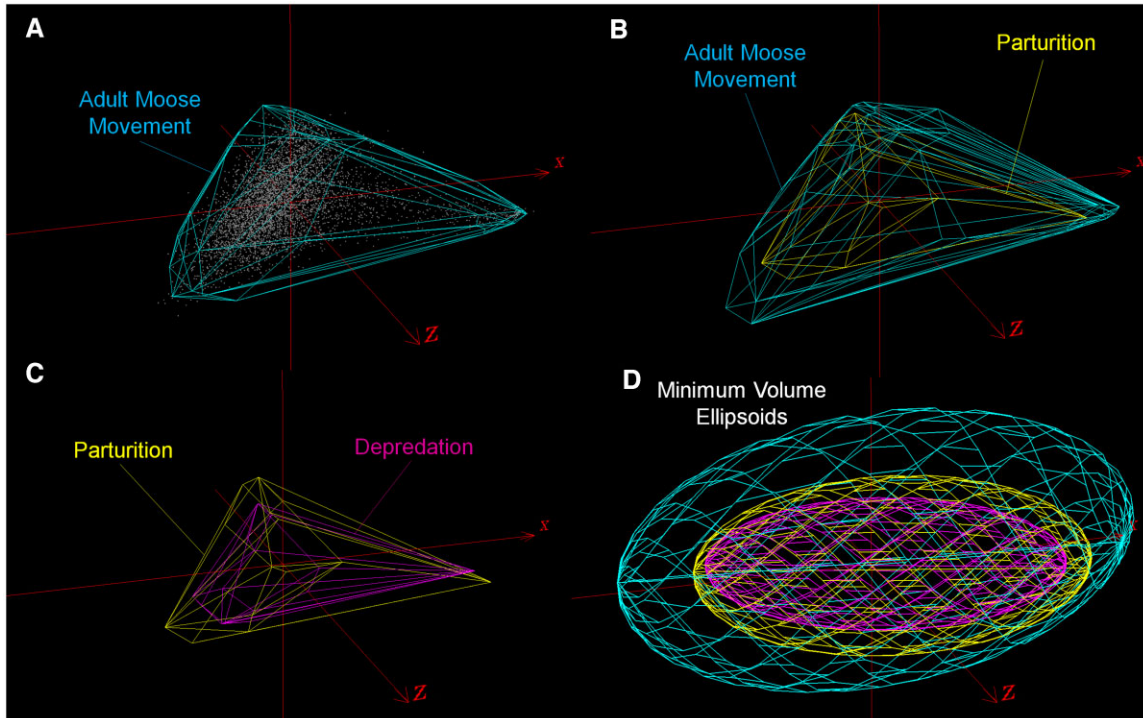
**Figure 2.** Moose distribution in environmental space. A principal component analysis was conducted on monthly EVI data from the study area from 2013 to 2020. Axis of each pane: X=Principal component one, Y=Principal component two, and Z=Principal component three. (**A**) Distribution of adult moose (blue polyhedron) and cloud of landscape conditions (i.e., monthly EVI data) summarized in the first 3 principal components. (**B**) Landscape conditions of sites of parturitions (yellow polyhedron) showing that calving occurs in a subset of landscape environmental conditions used by the adult population. (**C**) Sites of calf predation displayed by environment (pink polyhedron) showing that predation occurs in a subset of the landscape conditions where parturitions occur. (**D**) The environmental overlap of conditions where adults, parturitions, and predation attacks occur as shown by minimal volume ellipsoids of each phenomena. Here, predation nested in a portion of the conditions where parturition occurs, and parturition nested in a portion of the species realized niche.
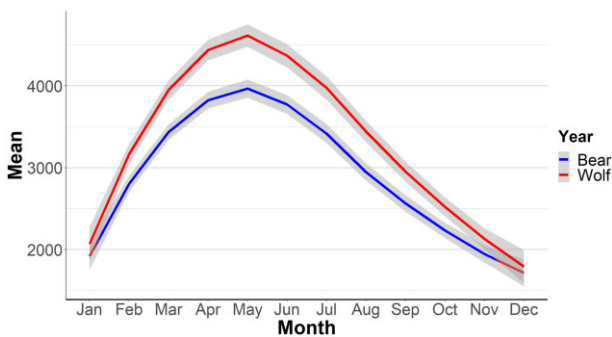


**Figure 3.** Average monthly EVI at locations of moose predation. The mean EVI value of each month across the study period (February 2013 to May 2020) at sites of predation by bears ($n = 22$) (red) and wolves ($n = 28$) (blue) was calculated across years. Peaks of primary productivity occurred in the month of May. There was also a disparity between overall EVI values between predator species, with bears predating moose in areas with lower average EVI values when compared with wolves ($t_{2669} = 7.46$, $P = 0.001$).

volume of the polyhedron in $n$-dimensional environmental space) have more unique characteristics and encompass more area in environmental space, than that of parturition, which took up less environmental space (Figure 2). Similarly, parturition was limited to a tractable, quantifiable, and predictable subset of the landscape used by the adult moose population. These results echo previous studies which have noted that pregnant female ungulates reduce or heavily alter their movement during seasons of parturition (Ciuti et al. 2006; Bongi et al. 2008; Long et al. 2009; Mcgraw et al. 2014;

Severud et al. 2015, 2019). Moose predation also occurred in specific and quantifiable landscapes and seasons. These landscapes corresponded with landscapes where parturition occurred (Figure 2C). In fact, calf mortality occurred almost exclusively within a subset of the EVI conditions where parturition occurred. These results show that EVI can be used as a variable through which the confluence or overlap of parturition and predation can be visualized. The interplay between parturition and predation within the landscape in terms of primary productivity also reflects previous assessments which have identified the important role that phenology and seasonality play in ungulate predator–prey systems (Metz et al. 2012; Stoner et al. 2016).

It is unclear whether or not parturition site selection by the cows was linked to predator avoidance or vegetation resources. Other ecological factors could drive landscape selection for parturition regardless of predatory risk, such as forage quality for the cow or vegetation for hiding of the newborn (Bowyer et al. 1999; William et al. 2018). Areas and seasons with higher relative EVI values, such as those revealed in our predation site assessment (Figure 3), could be favorable for parturition site selection but could also be more vulnerable to predation. In other words, the favorable landscape would function as an "ecological trap" whereby animals mistakenly favor landscapes which lower their fitness (Hale and Swearer 2016). In this ecological system, landscapes with high primary productivity (i.e., high EVI) draw cows away from landscapes that could ensure better calf survival. Both parturition and predation locations clustered under specific vegetation conditions (Figures 1 and 2), thus, it is unknown the extent to which predators could have lower success

rates and higher energy expenditure for predation if moose parturition sites were more scattered across the landscape. Other studies have suggested that moose cows practice natal philopatry (i.e., selecting similar areas for calving locations as their mothers; Colson et al. 2016), which could play a role in linking parturition and predation (Garneau et al. 2008; Montgomery et al. 2014). In fact, natal philopatry has been found to contribute to ecological traps by increasing predation in other species (Ekroos et al. 2012). Both wolves and bears are highly selective predators that disproportionately kill prey in vulnerable age classes (Husseman et al. 2003; Garneau et al. 2008; Montgomery et al. 2014). Furthermore, both wolves and bears have demonstrated movement shifts following moose parturition (Garneau et al. 2008; Montgomery et al. 2014), indicating a possible pattern of predators exploiting seasons or sites of parturition to access preferable prey. Conversely, the clustered nature of the parturition sites identified here could also drive predation patterns, as a higher density of neonatal calves in these locations could be leading to higher levels of mortality in this specific population. Future research could utilize landscape management strategies to develop a more scattered network of suitable calving locations across moose ranges, to assess how parturition site clustering, or lack thereof, impacts predation.

Our prediction of predation based on landscape configuration suggests that remotely sensed EVI data alone could be used to reconstruct the landscapes where moose parturition is likely to occur and, by extension, the landscapes where moose calves are likely to be killed by predators. This finding highlights the applicability of vegetation phenology data (e.g., EVI data) in predator–prey studies. As a remotely sensed variable, vegetation phenology could hold some advantages over more traditional landscape sampling methods. For example, vegetation phenology allows researchers to study surface areas on a systematic temporal basis, which could aid in landscape-change assessments. Remote sensing is also less intrusive than other field-based sampling methods and could mitigate risks of disturbance for species of interest. Identification of landscapes where parturition is likely to occur could also be valuable for managing landscapes for prey species of conservation concern such as the Minnesota moose population (Lenarz et al. 2010; Wolf et al. 2021). Future research lines could assess the feasibility of remotely sensed EVI data to identify sites that are conducive to calf survival, as parturition site landscape configuration has been shown to impact postnatal survival in moose (Severud et al. 2018). Furthermore, by using vegetation phenology data to reconstruct areas of parturition, managers could, by extension, be able to accurately identify where and when predation is likely to occur thereafter. These landscapes could then be used as suitable areas for predator population monitoring (e.g., camera trapping) or areas suitable for subsidizing predator species of value (Nevai and van Gorder 2012; Kuijper et al. 2016; Ciucci et al. 2020).

Several caveats and limitation were present in this study. Predators were not collared for this study, and therefore there was no tracking of the environmental, geographic, and temporal overlap of predators with prey. Predation localities, however, confirm predator presence and activity within the moose landscape. Future research could utilize predator movement data, and should include estimations of the landscapes across predator ranges by which the landscapes of prey movement can be compared. Additionally, inclusion of control sites where prey are present and predators are excluded could help compare effects of predator presence on landscape use. Furthermore, whereas we were able to identify the exact range of vegetation phenology values used by moose across areas

and periods, it is unclear what exact ecological factors made these specific landscape characteristics favorable for calf parturition (i.e., precise vegetation configuration or assemblage). We suggest that future research in northern Minnesota should assess fine-scale characteristics of landscapes identified in this study to elucidate what common variables might be present at each site (i.e., vegetation richness and diversity, fine-scale topography, animal community composition, etc.). Other environmental variables could also be included beyond EVI to ascertain an even more robust reconstruction of the physical landscapes moose occupy.

In conclusion, we found that the parturition and predation of moose calves in northern Minnesota does not occur at random. Instead, parturition occurred in specific landscapes and seasons which could be reliably reconstructed using remotely sensed vegetation phenology data. Predation occurred quickly thereafter in season, and occurred within a subset of these same landscapes. Landscape heterogeneity, as expressed here by variations in primary productivity of vegetation, contributed to predator–prey dynamics within the landscape, highlighting a continued need to understand the interplay between seasonality, vegetation primary productivity, and predator–prey dynamics. Finally, the results of this study highlight the utility of EVI as a unifying environmental variable for phenology-based studies to reconstruct wildlife interactions.

## Ethical Statement

All moose calf capture and handling protocols were conducted in accordance with the requirements of the Institutional Animal Care and Use Committee of the University of Minnesota (IACUC protocols 1410-31945A and 1803-35736A) and the guidelines recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

## Acknowledgments

## Funding

## Authors′ Contributions

L.E.E., S.A.M., and T.M.W. formulated the research question and developed the study design. S.A.M., T.M.W., E.J.I., Y.C.I., L.E.E., and P.V. collected the data. P.V. and L.E.E. conducted the analyses. P.V., L.E.E., S.A.M., and T.M.W. wrote the manuscript. All authors approved the last version of the manuscript.

## Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Supplementary Material

"Supplementary material can be found at https://academic.oup.com/cz".

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