Vegetation and local density are associated with red deer calving dates but don't explain the long-term temporal trend

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Abstract

Long-lived mammal species can show advancing reproductive phenology even though prolonged gestation means adaptive phenotypic plasticity to warmer springs, as observed for reproductive phenology across other taxonomic groups, is unlikely. A constraint model in which oestrus date depends on achieving a certain level of body condition seems more likely, so the question is which variables are promoting changes in condition? Here we investigated the role of food availability as a predictor of subsequent calving date in the individually-monitored red deer (*Cervus elaphus*) on the Isle of Rum, Scotland, where calving date has got 12 days earlier over 45 years. Food availability and competition were represented by three individual-level environmental variables: satellite-derived NDVI (a measure of greenness), local deer density and proportion of grassland, estimated within individual home ranges. Higher NDVI, lower density and higher access to grassland were all associated with earlier calving dates, supporting the hypothesis that higher resource availability increases individual condition, allowing earlier reproduction. Whilst the connection between resource availability and calving dates was clear, temporal trends in NDVI and density were weak and the associations explained a maximum of one day of the shift observed in calving dates. We discuss explanations for this contrast, including the potential that by eating NDVI, the deer generate error in its measurement. Regardless, we evidence that spatiotemporal heterogeneity in resources among individual home ranges contribute to the high variance observed in reproductive phenology. As a trait with consequences for fitness, this highlights the importance of incorporating spatiotemporal variation when considering broad-scale responses in a rapidly changing world.

Introduction

Shifts in the timing of seasonal life history events, or phenology, at mid and high latitudes have been widely reported in recent decades and are often attributed to ongoing climatic change (Cohen et al., 2018; Hassan et al., 2024). Phenological shifts have been most intensively studied in a few taxonomic groups, such as trees and birds. Temporal trends in phenological traits can often be directly or indirectly attributed to changing climatic conditions such as temperature, underpinned by organisms exhibiting adaptive plastic responses to inter-annual variation in environmental conditions (Cohen et al., 2018; Radchuk et al., 2019; Wolkovich et al., 2014). Whilst trends have been observed across a broad range of taxa, not all groups are likely to exhibit adaptive plasticity, with some more likely to be constrained by periods of suboptimal conditions and longer-term environmental effects than be responsive to environmental 'cues'. For example, mammals with prolonged and relatively fixed-duration gestations are highly unlikely to exhibit adaptive plasticity in birth dates with respect to local weather conditions (Gavrilets & Scheiner, 1993; Reed et al., 2010). Despite this, long-term phenological shifts have been recorded in some mammals that are of a similar magnitude to those of adaptively plastic taxa (Moyes et al., 2011; Renaud et al., 2019). Whilst it is well established that climatic conditions have changed in recent decades, we should not assume that temporal trends in phenology over similar periods are directly or wholly driven by the changing climate.

Within climate change research on phenological shifts there has been particular focus on the effects of temperature, and to a lesser extent precipitation, yet other environmental variables may also have an effect. Higher CO_2 levels, which indirectly contribute to warmer temperatures, can also have direct impacts on the biotic environment, for example by increasing plant growth and biomass (Maschler et al., 2022). The effect of CO_2 and

58 temperature on plant growth forms one component of ‘Global Greening’ which is being
59 observed to varying extents worldwide, including across mid- to high-latitude regions (Piao
60 et al., 2019). Increased plant growth has the potential to promote profound effects within
61 plant communities and cascading effects through trophic levels. Increased plant biomass
62 increases resource availability for herbivores, with potentially widespread implications within
63 and between species.
64
65 In particular, increased plant biomass has the potential to influence phenological traits in
66 herbivorous capital-breeding mammals. Species that fall closer to the capital-breeder end of
67 the capital-versus-income breeder spectrum rely more on stored resources to fuel
68 reproduction than income-breeder species; for example, species that gestate over winter at
69 mid to high latitudes experience limited resource availability through gestation (Stephens et
70 al., 2009; Williams et al., 2017). Individuals in better physiological condition (condition here
71 referring to their health and wellbeing) may begin their next reproductive cycle earlier than
72 those in poorer condition (Peláez et al., 2017). The effect of condition on reproductive timing
73 could contribute to variation in relative timing among individuals within a year as well as
74 variation in population mean timing among years. If higher plant biomass increases the
75 condition of individuals (Millán et al., 2022) and has increased in recent decades, then global
76 greening may be contributing to the observed shifts to earlier reproductive phenology
77 observed across a range of herbivorous mammals.
78
79 Satellite-derived data provides a relatively new window into spatiotemporal variation in
80 vegetation growth at scales impossible to achieve via manual monitoring (Kerr & Ostrovsky,
81 2003; Pettorelli et al., 2005). High resolution data on the spatial distribution of vegetation in
82 each year allows us to consider individual-level variation in resource availability; a very

challenging metric to attain, but of high importance for understanding within-population variation in a wide range of traits. Satellite imagery can be used to estimate the annual maximum greenness for each image pixel, often considered a proxy for the quality/volume of resource available to herbivores (Hamel et al., 2009; Pettorelli et al., 2011). A common metric derived from satellite imagery is the Normalised Difference Vegetation Index (NDVI), which indicates green cover and photosynthetic activity (Pettorelli et al., 2005). In the absence of vegetation community change, year-to-year variation in NDVI would represent differences in the volume/health of the vegetation that has grown. On the other hand, spatial variation in NDVI represents both differences in the volume of vegetation grown and differences between vegetation community types. Here we approximate variation in NDVI to vegetation availability. We hypothesised that higher vegetation availability would be associated with earlier reproductive phenology, as more resource would increase the condition of an individual (Millán et al., 2022).

Plant communities vary spatially such that diet preferences for particular communities lead to variation in the spatial distribution of herbivores. As a result, it is important to consider the effects of vegetation community (type) and resource competition, via local population density, alongside estimating the effects of vegetation availability on reproductive timing. Preferred grazing vegetation types may produce a large amount of plant biomass and therefore appear greener/have a higher NDVI, meaning that individuals spending the most time on preferred grazing also have high NDVI within their home range. On the other hand, preferred grazing areas are also likely to host higher local densities of herbivores (Gordon, 1989), with resource competition meaning each individual will receive less. By considering local herbivore density, vegetation type and the volume available in unison, we can begin to disentangle their independent effects which may be hard to identify alone, particularly if local

density, preferred grazing and vegetation availability covary strongly. We hypothesise that higher access to preferred grazing and lower local densities will be associated with earlier reproduction.

By considering environmental variables within individuals home ranges in each year, rather than at the population level, we are also able to test for consistent effects within and between individuals. If resource access within an individual's home range has a consistent impact on reproductive timing, then we would expect the effect to be similar both within and between individuals. Differences in the response within and between individuals would suggest that individuals may respond differently to variation in access to resources, or that variation in resource access has different effects on individuals living in distinct regions or periods of time. You could also consider effects partitioned in space and time, more explicitly testing for differences in the effect of spatial versus temporal variation in resource availability, which we include present fully in Supporting Information.

Here, we test the associations between resource access and reproductive timing in a population of red deer on the Isle of Rum. The population has shown a substantial shift in birth dates, with average calving dates shifting 12 days earlier over the past 45 years (Bonnet et al., 2019), however there is no clear or substantial effect of changing temperature, or other weather variables (Macphie et al., 2025). Within the study area, vegetation biomass and NDVI has increased over time (Butt et al., 2026). Plant growth through the summer prior to conception may influence conception dates via female condition acting as a constraint on reproductive phenology in this capital breeding species (Albon et al., 1983; Peláez et al., 2017). Prior work has not identified any association between total population density and

132 birth dates (Bonnet et al., 2019; Coulson et al., 2003), however this has never been explored
133 using individualised local density measures.
134
135 We capitalise on the unique resolution of spatial data available for the red deer study
136 population to consider access to resources at the individual level. Using satellite-derived
137 greenness data, annualised spatial local population density measures and local vegetation
138 mapping, we examine the effects of vegetation availability, access to preferred grazing and
139 local population density on birth dates within the individual home ranges of red deer. We test
140 the hypotheses that i) higher NDVI is associated with earlier reproduction, ii) higher access to
141 grassland is associated with earlier calving and that iii) higher density is associated with later
142 calving. We extend these hypotheses by testing whether the associations between birth date
143 and the focal environmental variables are consistent within and between individuals and in
144 space and time. Finally, we assess temporal trends in the environmental predictors to quantify
145 their contribution to the long-term trend observed in birth dates. Reproductive phenology has
146 important consequences for fitness and is highly variable (Bonnet et al., 2019).
147 Understanding the role of access to resources on reproductive timing in capital breeders sheds
148 light on how spatial heterogeneity in vegetation may drive variation in reproductive timing
149 within and between populations, and whether global greening is contributing to long-term
150 phenological shifts.
151
152
153 **Methods**
154 *Red deer data collection*
155 The population of red deer resident within the north block on the Isle of Rum have been
156 studied at the individual level since 1972 (Clutton-Brock et al., 1982). In Scotland, red deer

mate in September-November and calve in May-July after a gestation of around 237 days (Clements et al., 2011). On Rum, females are observed daily in the run-up to calving to accurately record birth dates, and calves are caught and tagged soon after birth, meaning they can be identified throughout life. Here, the calendar dates of birth dates were converted to ordinal dates for analysis, with 1st January = 1. Births were restricted to those falling between ordinal dates 121 - 212 (1st May - 31st July in non-leap years), removing 2% of records, consistent with previous analyses of birth date in this system (Macphie et al., 2025; Moyes et al., 2011; Froy et al., 2019). All deer are monitored throughout the year meaning that the reproductive status of females and survival of calves is known. In the study population, females do not necessarily breed every year, and calves survive for different periods. Reproductive status describes the reproductive effort of a female over the year preceding the birth date of interest. If the birth date related to a female's first calf they were 'naïve', if they had previously calved but not in the previous year they were a 'true yeld', if they had a calf the previous year and it survived until 1st May the following spring they were a 'milk hind', if the calf died after 1st October they were a 'winter yeld' and if the calf died before 1st October they were a 'summer yeld'.

Population censuses are carried out across the study area roughly weekly through January-May, July, September and November each year, resulting in roughly 40 censuses per year. Each individual is recorded to the nearest 100m easting and northing national grid reference within each census. We included identified deer of both sexes and all ages seen in each census; if an individual was recorded multiple times in a census only the first record was used and unidentified individuals (4%) were removed from our analyses. The census observations were used to estimate the spatial pattern in local density within each year and to estimate each individual's home range within each year.

Annualised spatial pattern in local density

We required an annualised spatial pattern of deer density, representing the average space use of deer. As each population census depicts the distribution of deer at a given point in time, we estimated population density at the census level and averaged across all censuses within each year. As no census can fully capture the entire space use of the deer, we used two-dimensional (2D) Kernel Density Estimates (KDE) to quantify the probability distribution of deer within each census using the sparr package (Davies et al., 2018) in R version 4.5.1 (R Core Team, 2025). This package estimated the probability distribution of deer within the bounds of a shape file, allowing us to confine the distribution of deer to land. For each census, the grid references of the observed deer were used to produce a 2D probability distribution of deer. The probability distribution (which sums to one across the site) was multiplied by the number of deer within the census, meaning the summed probability across the site for each census equalled the total number of deer observed. We took the mean spatial pattern of deer density across all censuses within each calendar year as annualised estimates of the spatial distribution of deer. The annualised estimates of deer density therefore incorporated year-to-year variation in total population size. The average distribution of density across the site is shown in Figure 1c. We fixed the bandwidth for all census KDE's to the average bandwidth estimated across all censuses; see Supporting Information for more details. The minimum number of deer recorded within a census was limited to 50, chosen following sensitivity analysis comparing the KDEs estimated with varying numbers of deer recorded; see Supporting Information for more details.

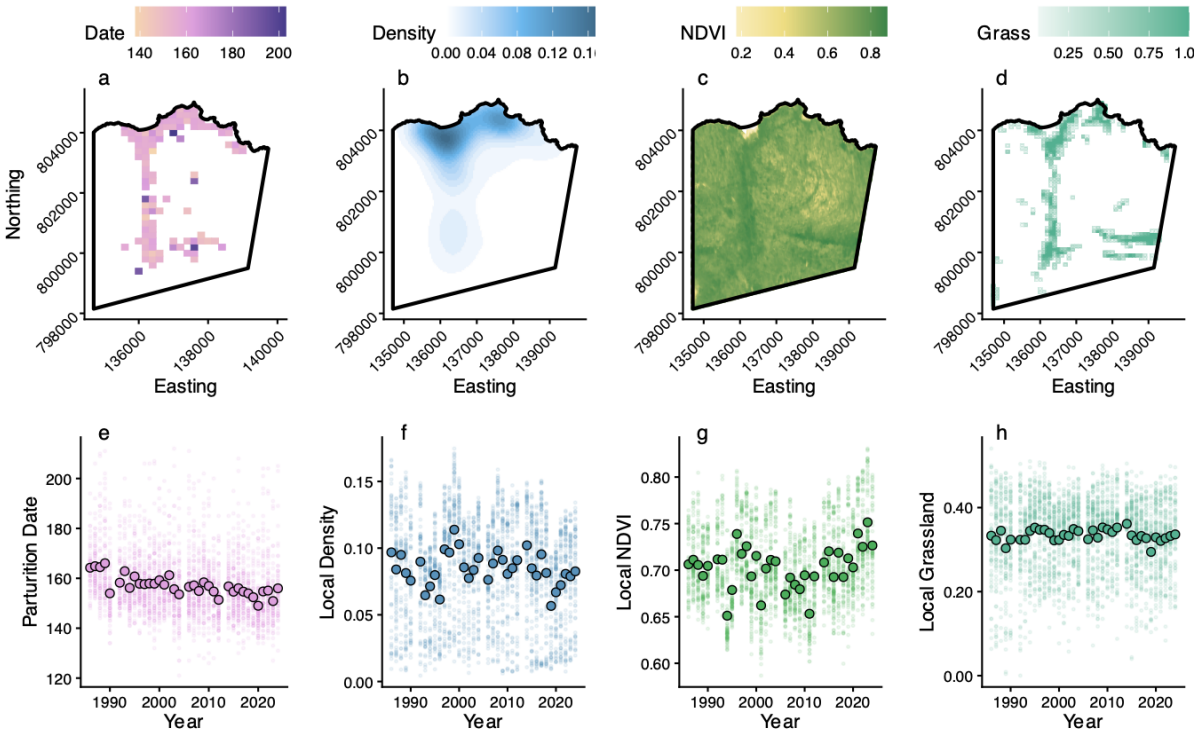

Figure 1: Average spatial distributions of birth dates, population density, NDVI and grassland habitat, and temporal patterns in the individual-level data for each variable. Study area maps show a) the average birth date per 200m square (larger resolution to aid visibility), b) estimated average population density distribution across years from 2D kernel density estimator, c) average maximum NDVI across years within each 30m satellite image pixel and d) Distribution of grassland across the site by proportion cover within each 100m grid cell. Temporal trend plots (e-h) show the raw birth date data and annual estimates of local density, NDVI and grassland within each individual's home range in the previous year; larger points show the annual mean. NDVI data was missing for the year preceding 1991, 2005 and 2013, meaning these years were not included in our analyses.

Satellite imagery data

Satellite imagery data was extracted for 1984-2023 across the study area from Google Earth Engine-hosted Level-2 Collection-2 Tier-1 Landsat 5 (Thematic Mapper [TM]), Landsat 7 (Enhanced Thematic Mapper Plus [ETM+]), and Landsat 8 (Operational Land Imager and

Thermal Infra-Red Scanner [OLI-TIRS]) and processed using the LandsatTS R package (Berner et al., 2023). The satellite data was used to calculate the NDVI in each Landsat image with a spatial resolution of 30m per pixel, allowing high resolution estimation of the spatial variation in NDVI in each year. LandsatTS was used to calibrate the different satellites and estimate the maximum NDVI in each pixel in each year, for more details see Butt et al. (2026); the average NDVI in each pixel is shown in Figure 1b. Landsat data was extracted for a larger area than in Butt et al. (2026) to incorporate more of the area in which deer have been observed during censuses.

Due to high cloud cover, the NDVI could not be estimated for some pixels in each year through the LandsatTS package. Years with less than 75% pixel coverage for NDVI estimates were removed from the analyses (1984, 1990, 2004 and 2012). Missing pixels in the remaining years were imputed using a model in R-INLA (Rue et al., 2009); 78% of years required imputations of <1% of pixels, 11% of years required 1-5% pixel imputation and 11% of years required 14-21% pixel imputation. The model included random terms of year, pixel identity and a Stochastic Partial Differential Equation (SPDE) to account for spatial-autocorrelation. The NDVI of pixels missing NDVI estimates in each year were predicted incorporating all model terms. Predictions for the observed pixels in each year correlated highly ($r = 0.92$) with the maximum NDVI estimates from LandsatTS. The NDVI was averaged within each 100m grid-cell to align with the spatial resolution of the deer census data.

240 *Local vegetation type data*

241 Local vegetation was described by a base map of the vegetation available from the
242 NatureScot Spatial Data Hub (Bates et al., 2002). Within the map, polygons identified
243 National Vegetation Classifications at the subcommunity level (55 subcommunities). These
244 were aggregated into eight main subcommunities: acid grass, blanket bog, calcareous grass,
245 dry heath, maritime cliff, poor dry grass, wet grass, and wet heath; non-vegetative areas
246 remained unclassified, e.g. Kilmory beach. Wet heath and blanket bog dominate large parts of
247 the study area (Moore et al., 2015). Smaller patches of grassland; categorised above as acid,
248 calcareous, poor-dry and wet, are preferred by the deer for grazing (Gordon, 1989) and
249 therefore were the focal vegetation types of our analyses. One vegetation map is available,
250 meaning the distribution of vegetation in our analyses was held constant in time; the
251 distribution of vegetation types is not believed to have change substantially over the past 40
252 years.

253

254 The vegetation map was aligned with the NDVI data and both were aggregated at the 100m
255 grid-cell scale. The proportion of each 100m grid-cell that contained a grassland vegetation
256 type was used in our analyses (Figure 1d).

257

258 *Annualised individual home ranges*

259 A similar approach to the spatial pattern in local density was used to estimate each
260 individual's annual home-range as a probability distribution. All census points for an
261 individual in a given year were used to produce a 2D KDE representing that individual's
262 space use in that year. The distribution is broken down into grid-cells across the study area
263 (shape file), with each grid-cell assigned a probability of the deer being found there. The grid-
264 cell recording the highest probability was recorded as the 'centroid' of the individuals home

range in that year, for use in testing for spatial autocorrelation. For each deer:year combination, the KDE bandwidth was fixed at the mean bandwidth estimated across all deer:year combinations. The minimum number of observations for a deer within a year was 10, chosen following sensitivity analysis comparing the KDEs estimated with varying numbers of observations; see Supporting Information for more details. We ran our main calving date models using a 5, 10 and 15 observation threshold to assess any impact this had on our results; results for the 5 and 15 observation datasets were consistent with our main analyses using 10 observations (Figure S4). The probability of the range for each deer:year was summed at the 100m grid-cell level to spatially align the estimates with the satellite imagery and vegetation type data.

Annualised individual estimates of vegetation and density

The data for NDVI in a given year, density in a given year and grassland (consistent across years) were overlayed with an individual's annual home-range. For each grid-cell, the probability of occurrence was multiplied by each spatial environmental variable and summed across the grid. This produced an individualised home-range weighted estimate of each environmental variable in each year (Figure 1f-h). NDVI and density varied within individuals in different years due to a combination of the annualised spatial environmental data and differences in the home-range of the individual, whilst differences in access to grassland differ purely due to differences in home-range. We explored the correlations between the NDVI, density and grassland among home-ranges, illustrated in Supporting information.

Main birth date analyses

To assess evidence for an association between birth dates, vegetation availability (NDVI), access to preferred grazing (grassland) and local density, we used linear mixed effects models to test environmental variables in one year as predictors of birth date in the next year (representing resource availability in the summer prior to conception). We included all three environmental variables in the same model, which allowed us to assess evidence for the effect of each whilst the other two were accounted for. The three environmental variables were mean centred and scaled: local NDVI mean = 0.70 (SD = 0.04); local density mean = 0.08 (SD = 0.04); local grassland mean = 0.33 (SD = 0.09). The models of birth date also included core fixed effects of year, female age and age^2 as continuous variables and the categorical reproductive status, and random terms of year and female ID (Froy et al., 2019; Macphie et al., 2025). The year continuous fixed effect was included to allow for additional sources of the temporal trend in calving dates, preventing biased slope estimates when there is a temporal trend in a continuous predictor (Iler et al., 2017; Macphie et al., 2025). A model containing the core terms but none of the environmental variables was run to assess the temporal trend in the dataset used. Each environmental variable was also modelled independently of the other two, presented in Supporting Information.

Decomposition of environmental predictors

To consider the processes underlying the identified associations between birth dates and the environmental variables, we decomposed the effects of the environmental predictors within and between individuals. We included all three variables in the decomposition models, decomposing each variable in different models to avoid over-parameterisation. Decompositions in space versus time are presented in Supporting Information.

To decompose within and between individuals, the average of each environmental variable for each individual was calculated across their reproductive years and included as the between-individual variable, capturing longer-term plasticity, selective (dis)appearance and microevolutionary change (Boutin & Lane, 2014; Charmantier & Gienapp, 2013; Froy et al., 2019). The annual deviations from the average for each individual were used as the within-individual variable, capturing the individual variation in response to varying environmental conditions. To estimate the difference between the within and between slopes, the undecomposed variable and the between individual variable were included in the same model as in van de Pol & Wright (2009). The slope estimate for the between individual variable then describes the difference between the slopes.

Temporal trends in environmental variables

To assess the extent to which any identified effects of local NDVI, density or grassland explain the substantial linear temporal trend observed in parturition dates, we assessed the presence of linear temporal trends in the annual individual home range estimates of each environmental variable. We also consider trends across years in the between-individual (individual mean) variable, which could reflect both a change in the way space is used and temporal trends in the variable. We did not consider temporal trends in the within individual variable as it is centred on zero for every individual, such that the mean over time cannot change.

We also used a linear model to analyse any long-term trends in population size, distinct from local densities within individual home ranges. The average number of individuals observed within a census in each year was regressed against year. The temporal trend in NDVI across the study area was recently analysed, finding a modest yet significant increase in NDVI over

time in all vegetation types, with a slightly stronger trend in the grassland areas (Butt et al., 2026).

In-situ vegetation sampling comparison

In situ vegetation sampling has occurred at six grassland plots across the study area since 1987. We used this data to compare estimated effects of annualised *in* situ vegetation data on calving dates to results from the individualised satellite data. The *in situ* data also allowed us to consider plant growth, or productivity, in addition to the standing crop (uneaten vegetation) which more closely resembles NDVI. Full details can be found in Supporting information.

All main analyses, excluding the *in situ* sampled vegetation, were Gaussian models carried out in R-INLA under R version 4.5.1 and residuals were checked for normality and independence. We used dHARMA to test the residuals of each model for spatial autocorrelation (Hartig, 2025) and, where identified, models were run again including a SPDE term. Half-cauchy priors with a scale of 10 were used for random terms and penalised complexity priors were used for a SPDE terms with a 0.05 probability that the range was larger than 2km.

Results

Correlations between local NDVI, density and grassland

Correlations between the three home-range weighted variables showed a moderate negative correlation between NDVI and density of -0.57 and between NDVI and grassland of -0.49, whilst density and grassland showed a stronger positive correlation of 0.72. Further investigation showed the negative correlations were contributed to by differences in local

density between the north and south of the main glen in the study area, paired with spatial patterns in the distribution of grassland and NDVI (Figure 1, S1).

Main birth date analyses

NDVI, density and grassland all showed significant associates with calving date (Figure 2). Higher NDVI was associated with earlier calving dates (posterior mean [95% credible]: -1.11 [-1.75 – -0.48]; Figure 2a, 3a), higher density was associated with later calving dates (0.95 [0.21 – 1.68]; Figure 2b, 3b) and higher access to grassland was associated with earlier calving dates (-0.87 [-1.50 – -0.24]; Figure 2c, 3c). Across the range of each environmental variable experienced among individuals, local NDVI explained 6.58 (2.86 - 10.29) days of variation in birth date, local density explained 4.28 (0.93 - 7.62) days and local grassland explained 5.31(1.45 - 9.16) days; birth dates vary by 91 days in the data set used. When modelled independently, no significant effect of grassland was identified (Figure 2, Supporting information); we believe this was due to the strong positive correlation with local density, which has an effect in the opposite direction. The independently estimated density effect, however, was very similar to the partial slope estimate (Figure 2).

Decomposition of environmental predictors

Slope point estimates and posterior distributions were similar between the within and between and complete variables for all three environmental variables (Figure 2). The association between birth dates and each environmental predictor did not differ within and between individuals (NDVI = -0.29 [-1.43 – 0.85]; density = -0.28 [-1.66 - 1.10]; grassland = -0.80 [-2.01 - 0.40]). Uncertainty in the slope estimates increased (Figure 2), particularly for the within-individual slopes. Two factors likely contribute to the increased uncertainty i) there is likely more error in the within-individual predictor because inter-annual variation in NDVI

is less certain, with only one observation per year, than spatial variation in NDVI which averages across all years, and ii) the within-individual deviations covering a smaller range of values than the individual averages. Decompositions of NDVI and density were consistent in space and time, see Supporting Information for details.

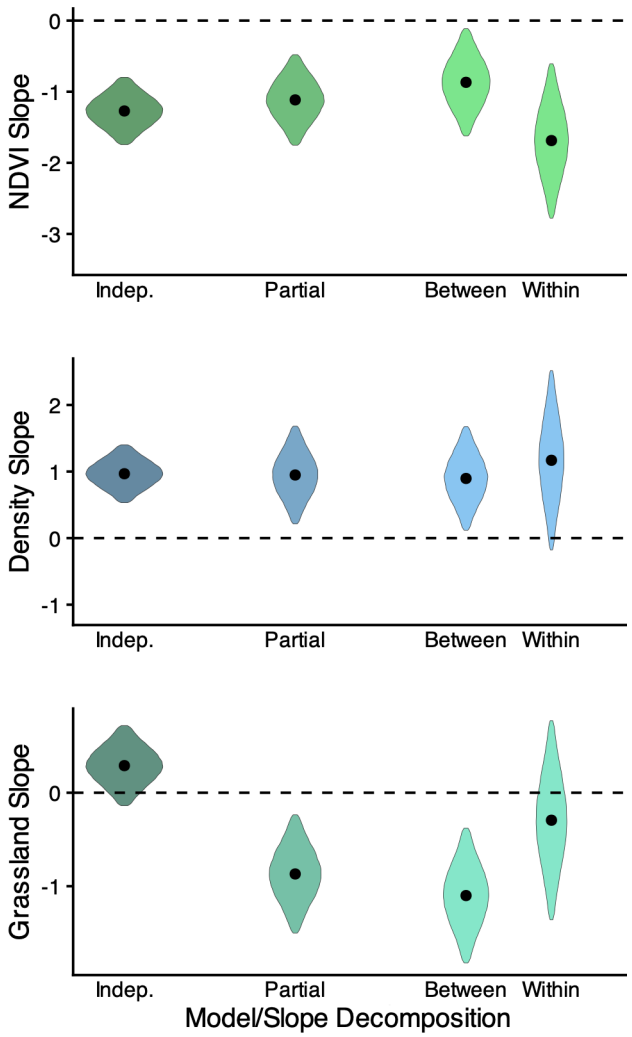

Figure 2: Slope estimates for the association between red deer birth dates and a) local NDVI, b) local density and c) local grassland. Violin plots show the posterior distribution of the slope estimate within the 95% credible intervals; black points indicate the posterior mean. Different estimates along the x-axis show were attained when modelled independently, with all three environmental predictors in the same model (partial slopes) and when decomposed within and between individuals.

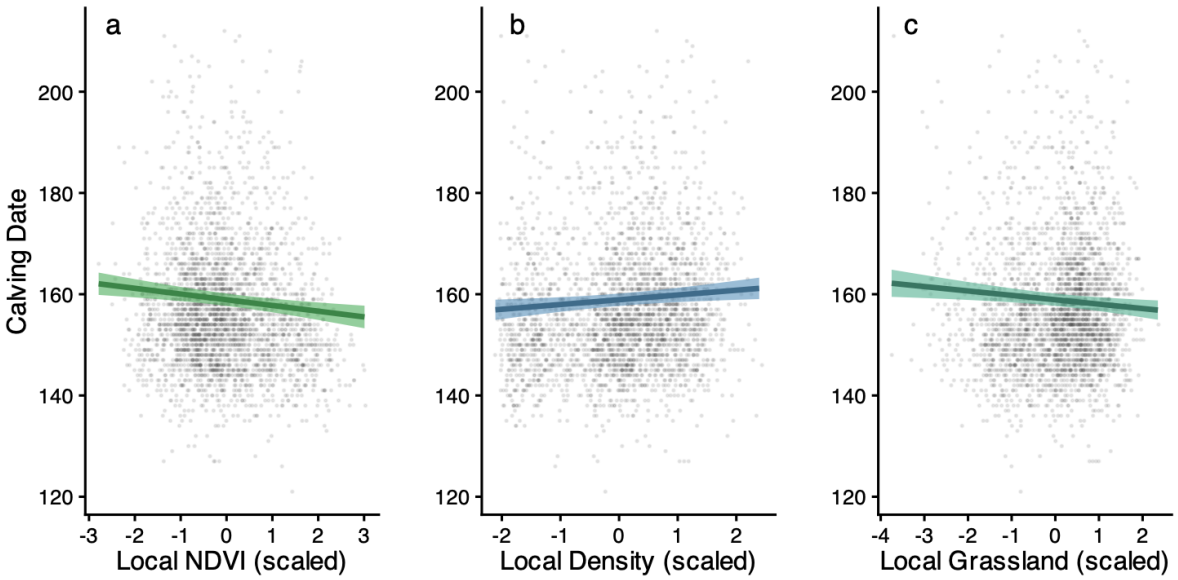

Figure 3: Model slope estimates with 95% credible intervals (CIs) for the association between red deer calving dates and a) local NDVI, b) local density and c) local grassland. The three slopes were estimated within the same model.

Temporal trends

There was a significant temporal trend within the birth date data used in our analyses of -2.68 (-3.49 – -1.87) days per decade, equating to birth dates getting earlier by 10.18 (-13.26 – -7.11) days over the 39 years, consistent with previous studies (Bonnet et al., 2019; Coulson et al., 2003; Moyes et al., 2011). For temporal trends in our environmental predictions, the coefficients presented relate to the predictor and response variable both having been scaled, unless otherwise stated. Despite an increase in NDVI across the study area (Butt et al., 2026), the signal of an increase in the NDVI within individuals' home ranges was less clear (0.13 [-0.04 – 0.30]), with credible intervals overlapping zero, albeit with a 0.94 probability of a positive slope. The signal of an increase in NDVI over time was clearer when considering the average NDVI experienced by individuals across the years in which they reproduced (0.09 [0.01 – 0.16]), meaning that individuals alive in recent years on average experienced higher NDVIs within their home ranges then individuals in the past.

The number of deer recorded at censuses within each year has reduced on average by 15.38 (7.75 – 23.00) deer per decade over time, resulting in an estimated decline in population size of 58 individuals or 24% over 39 years. This decline is reflected in the local densities within individual home ranges (-0.13 [-0.24 – -0.02]) and the average density of individuals' home ranges across the years in which they reproduced (-0.10 [-0.13 – -0.07]). The proportion of grassland within home ranges may have slightly declined over time (-0.03 [-0.07 – 0.00]), with a 0.96 probability of a negative coefficient.

Whilst temporal patterns are observed within each environmental predictor among annual individual home ranges, either within the complete variable or the decomposition, the magnitude of the trends identified were remarkably small. As the coefficients are relative to scaled variables, the slopes presented equate to the number of standard deviations (s.d.) of change in the environmental predictor for a 1 s.d. change in years (equating to 11.15 years). This means that both NDVI and density within each individuals annual home range was estimated to increase by just 0.45 s.d. across the entire study period. As a result, the ability of these predictors to explain the temporal trend in parturition date was minimal. Multiplying the point estimate for the total predicted change in each complete environmental variable across the years studied by the point estimate for the association between each complete environmental variable and birth date (from the model containing all three) shows that just -0.51, -0.42 and -0.10 days of change in birth date would be predicted by local NDVI, density and grassland, respectively over the 39 years.

In-situ vegetation sampling

The in-situ sampled vegetation data did not show any significant associations with calving dates. The standing crop had increased over time by 0.7g (SE = 0.2g) per $1m^2$ per year. Our approach used total standing crop, summed throughout the year, and shows a shallower slope than was found when looking at the peak months of June and July (Butt et al., 2026).

Discussion

Our study has shown clear associations between calving dates and all three environmental variables (Figure 2). Earlier calving dates were associated with higher NDVI, lower density and higher access to grassland, explaining 6.6 and 4.3, and 5.3 days of variation in birth dates within our data, respectively. The decomposed variables showed that the effects are consistent within and between individuals, and NDVI and density effects were consistent in space and time. Taken together, our results indicate that higher access to food during the year of conception is generally associated with earlier birth dates in the following year. Whilst the connection between vegetation and birth dates is clear, the lack of strong temporal trends in the environmental variables explored indicates that, as measured, they do not contribute much to the substantial shift in birth dates that has been recorded in the population over the past 40 years.

Our result relating higher NDVI to earlier parturition dates is consistent with the hypothesis that more vegetation increases individual condition (Millán et al., 2022), allowing females to come into oestrus earlier in the autumn. Higher NDVI, or greenness, should reflect more and/or healthier vegetation biomass, though it will also be influenced by variation in the plant community. If variation in NDVI that results from different vegetation communities drove the

identified effect, we would expect to see a shallower slope within-individuals compared to between, as the space use of deer varies more among individuals than within. Therefore, the consistency in slopes estimated within- and between-individuals and in space and time suggests that the volume and health of vegetation is likely to dominate the effect. This is also supported by the slightly weaker signal identified for the effect of access to grassland, which could not be detected when density and NDVI were not accounted for. Higher biomass during the summer prior to birth is also likely to correlate with higher biomass available overwinter, so the effects of higher NDVI throughout the main growing season may transcend the period over which it can be estimated. Higher resource availability throughout the winter has the potential to reduce gestation length if mothers are better fed during gestation (Clements et al., 2011).

Previous work at the population level found no association between population density and birth dates (Bonnet et al., 2019; Coulson et al., 2003), however when considering local density at the individual-level we do see such an effect. Higher density was associated with later birth dates, consistent with the hypothesis that when the available food is shared among more individuals, each receives less, reducing condition and delaying oestrus.

In a greening environment the use of space by animals may change. Areas that previously had low food availability may now have more, or areas of high previous food abundance may have less. Alongside changes in food availability, we might hypothesise that home ranges and the use of space by a population will change to reflect the pattern of resource, particularly at high densities when resources are more limited. The negative temporal trend we identified in the average spatial NDVI of occupied home ranges was very small but does suggest some change in space use between the past and present. The ranges occupied more recently include

areas that on average over time have had slightly lower NDVIs than ranges occupied in the past. This may represent individuals spreading out into areas that previously had less food and now have more. The grassland habitats across the study area have had slightly higher increases in NDVI than other habitats (Butt et al., 2026). It is likely that some areas with non-grass vegetation types also contain some grasses, particularly those neighbouring the grasslands. If grasses are particularly benefiting from the climatic changes experienced in the area, then these areas may become increasingly appealing to the deer despite representing a less desirable vegetation type on average. Whilst the trend in NDVI across ranges may suggest some change in space use, the density results do not necessarily support this. There was no temporal trend seen in the average spatial density of home ranges, meaning that individuals have not begun to occupy areas that have generally supported fewer deer. Further analyses of space use in response to greening may shed light on an alternative spatial consequence of the changing climate.

Whilst our results have identified novel associations between vegetation, density and birth dates, they do not explain the substantial temporal trend in birth dates that has been observed. One reason for this could be that variation in NDVI only represents a fraction of the variation in food that has been available to the deer. NDVI measures the greenness of the vegetation that has not been eaten, whilst the deer continue to eat new growth as it is produced. The temporal trend in plant growth may be far more substantial than can be estimated by satellite. Working out the extent to which this occurs would pose many challenges, as the rate of plant growth may respond to herbivory (Georgiadis et al., 1989), meaning that cage studies such as ours may also underestimate the growth occurring in preferred grazing habitats. Using the *in situ* vegetation sampling data from our study site, we found no increase in grass productivity over time, however the error in this metric will be high because it combines two samples. We

do see an increase in the standing crop over time, which is just one sample, however this did not predict calving dates. The absence of evidence for an effect of annual standing crop on calving date, paired with the previous absence of an effect of annual population density, suggest that the individualised metrics we have developed for local NDVI and density are important in detecting the effects of these variables on calving date. When using annualised predictor variables, the error at the individual level will be substantially higher, reducing the slope estimates and increasing the uncertainty. There will also be substantial error in our local density and NDVI variables, particularly for NDVI when considering that it would ideally represent what has been consumed. As such, our slope estimates may also be reduced in magnitude and show increased uncertainty, reducing our ability to accurately quantify the temporal trend in the trait that should be explained. Nevertheless, our results suggest that greening across the site does not contribute substantially to the observed temporal trend in calving dates, similarly to changing temperature (Macphie et al., 2025). With growing evidence that the temporal trend is not explained by plasticity in response to environmental change, perhaps a genetic response is more heavily involved than could previously be identified (Bonnet et al., 2019).

Our study has identified associations between vegetation availability and birth dates in red deer consistent with the hypothesis that more food increases individual condition bringing them into oestrus earlier. The effects of vegetation were similar within and between individuals and in space and time, suggesting that the availability of vegetation in general may be more important than particular vegetation types, within the variety of home ranges occupied across our study site. Whilst this has not explained the temporal trend in birth dates observed in our population, it shines an interesting light on how spatiotemporal variation in plant biomass is likely to influence variation in reproductive phenology within and between

populations. Within climate change ecology research, it is important that we continue to consider environmental conditions beyond temperature and precipitation. Increasing plant growth and variation among plant species and communities is likely to have substantial consequences for the herbivores that rely on them, with cascading effects through trophic levels in space and in time.

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Author Contributions

Kirsty Macphie and Josephine Pemberton conceived the ideas with support from Hannah Froy and Loeske Kruuk. The field project methodology was led by Tim Clutton-Brock, Josephine Pemberton and Fiona Guinness. Alison Morris, Sean Morris, Fiona Guinness, Josephine Pemberton and Tim Clutton-Brock collected the field data and Shane Butt collated the satellite data; analysis was led by Kirsty Macphie; Kirsty Macphie led the writing of the manuscript with support from Josephine Pemberton. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

There are no conflicts of interest.

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Supporting Information for: Vegetation and local density are associated with calving dates in red deer but don't explain the long-term temporal trend.

Sections:

1. KDE bandwidths
2. Correlations between local NDVI, density and grassland
3. Modelling each environmental variable independently
4. Decomposing local NDVI and density in space and time
5. Association between calving dates and annual in situ vegetation sampling
6. Sensitivity analysis for threshold number of observations

1. KDE bandwidths

As part of the KDE estimation a bandwidth is used to control the level of smoothing, and the sparr package (Davies et al., 2018) contains a function to estimate a suitable bandwidth for the datapoints provided. The number of observations varies among censuses, which influences the estimated bandwidth in addition to the spread of the points. The variation in bandwidth is probably partly the product of spurious variation due to chance in the number of individuals observed, though it will also incorporate some biological meaning. For consistency within this study, we chose to fix the bandwidth for all census KDEs at the mean bandwidth estimated across all censuses in all years.

2. Correlations between local NDVI, density and grassland

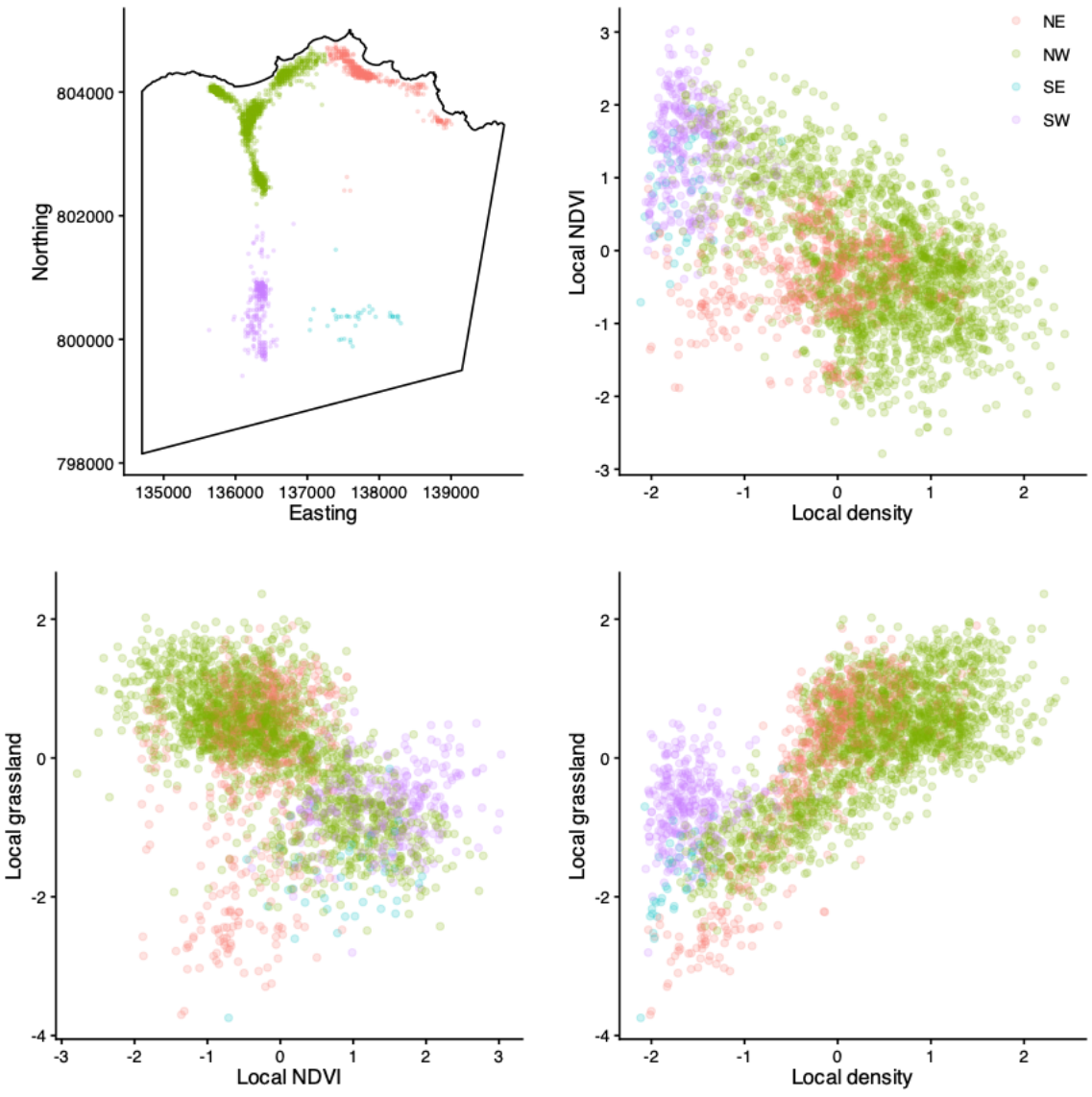


Figure S1: Correlations between local NDVI, density and grassland within individual's home ranges, coloured by spatial groupings (N=north, S=south, W=west, E=east).

3. Modelling each environmental variable independently

When modelled independently, NDVI and density both significantly predicted birth dates (Figure 2a,b). An increase in NDVI was associated with earlier births (posterior mean [95% credible intervals]: -1.27 [-1.75 – -0.80]) and an increase in density was associated with later births (0.97 [0.53 – 1.40]). There was no evidence for an effect of grassland on calving dates (0.36 [-0.06 – 0.78]), though the point estimate was positive – suggesting higher access to grassland was associated with later calving dates, which would be counter to our expectations. The grassland slope estimate changed when all three environmental variables were included in the same model, see main text.

4. Decomposing local NDVI and density in space and time

Different responses to variation in resource access in space and time would suggest that the metric of resource access itself is unlikely to explain the full effect identified and different processes are occurring in space versus time. We decomposed local NDVI and density into a spatial average and annual deviation for each annual home range. Access to preferred grazing was only decomposed within and between individuals because the vegetation map is constant in time meaning there is no temporal deviation. To decompose the NDVI and density in space and time, we worked out the average NDVI and density in each home range across all years and the annual deviations from this. To do so, we estimated the NDVI and density in every annual home range in every year, not just the year in which the deer occupied that range. From this, the mean value for each home range across all years could be taken as the spatial variable, with differences between home ranges purely attributed to the space they occupy. The deviation of the relevant annual value from the spatial average was used as the temporal variable, describing how each range in the year experienced deviated from the spatial

763 average. The spatial average and annual deviation for each home range were included as
764 fixed effects, and the spatial average and complete variable were used to test for a differences
765 between the effects in space and time as in van de Pol & Wright (2009).
766
767 We tested for temporal trends in the spatial average and temporal deviations of the of local
768 NDVI and density from the spatiotemporal decomposition. Any trend across years in the
769 temporal deviations would be expected to be similar to the overall trend, unless there has
770 been a change in the spatial pattern of the environmental variable. A trend across years in the
771 spatial average would suggest a change in the home ranges used, moving towards home
772 ranges with generally either higher or lower average NDVIs or densities than in the past.
773
774 *Results*
775 Decomposing local NDVI and local density in space and time showed similar slope estimates
776 to the complete variables (Figure S4), with no significant differences between the slopes for
777 NDVI (0.76 [-0.84 - 2.35]) or density (0.40 [-1.09 – 1.89]). Uncertainty in the time slopes
778 was higher, probably due to higher error and the smaller range of values among the temporal
779 deviations in local NDVI and local density compared to the spatial averages.
780
781 There was a strong a suggestion that that the annual deviations of individual home ranges
782 increased over time (0.16 [0.00 – 0.32]), with a 0.97 probability of a positive slope. An
783 increase in the annual deviations of home range NDVI would indicate that in more recent
784 years the NDVI within a given home range is higher than it would have been in the past.
785 Conversely, the spatial average NDVI of home ranges occupied slightly decreased over time
786 (-0.03 [-0.05 – -0.01]), which may contribute to the increased uncertainty in the temporal
787 trend in NDVI across home ranges compared to the study site as a whole (Butt et al., 2026). A

decrease in the average NDVI of occupied home ranges suggests that individuals living in more recent years are living in areas that are less green than individuals in the past, however the effect size is very small. The annual deviations of home range density from the spatial average had declined over time (-0.13 [-0.23 – -0.03]), similarly to the complete local density variable. There was no trend in the spatial average densities of home ranges (0.00 [-0.02 – 0.02]).

5. Association between calving dates and annual in situ vegetation sampling

Since 1987, vegetation growth has been consistently sampled across six grassland plots. At each plot, two cages measuring 0.5 x 0.5 m were used to exclude grazing. Each month, from March-November each year, the vegetation from five 10 x10 cm quadrats was picked to root level both inside and outside each cage. The cages were randomly repositioned within each plot each month to ensure the same location was not sampled repeatedly. Roughly 20% of the sample for each plot inside or outside the cages was sorted into categories of: live vegetation, comprising herbs and grasses, dead vegetation, moss and heather. Each subsample and the remaining vegetation were dried and weighed. The total dry mass per category was calculated by their proportional composition within the subsampled portion. Here we focus on the live category as the preferred food source of the deer. For further details on the vegetation sampling see Butt et al. (2026).

We used two metrics from the vegetation sampling to analyse associations with calving dates: productivity and standing crop. The productivity was calculated by subtracting the dry mass of vegetation outside the cages in one month from the dry mass of vegetation inside the cages in the following month, representing the growth that occurred in the absence of grazing. The

standing crop is the term used to describe the dry mass of vegetation outside of the cages. Standing crop is expected to be more comparable to the satellite-derived NDVI measures, as it represents the vegetation available to the deer at the time of sampling.

We required an annualised metric of productivity and standing crop to use as a predictor of calving dates. We used the data at the annual rather than plot level as the six plots do not represent different individuals' home ranges. To represent the food available to deer throughout the year prior to calving, we summed the average monthly productivity and standing crop within each year. Across all plot:month:year combinations, 2% of samples were missing (see Butt et al., 2026). To account for this, we modelled the average productivity and standing crop in each year and month using linear mixed models in lme4 (Bates et al., 2015). Productivity or standing crop from each plot in each month in each year were the response variables and year was included as a fixed effect to quantify any temporal trend. Random terms included year, month, each month in each year and plot. The fixed effects and random effects for year, month and each month in each year were used to calculate the predicted average productivity and standing crop in each year in each month. For the months:years with sampled data, the predicted mean productivity and standing crop both had extremely high correlations with the means calculated from the raw data (0.99). The monthly means were summed within each year, giving an annual estimate of productivity and standing crop. Productivity and standing crop were each included in separate linear mixed models of calving date, in addition to all other core terms consistent with previous models.

6. Sensitivity analysis for threshold number of observations

Effect of number of observations on KDE estimates

We performed some sensitivity analyses to determine a sensible cut off for the minimum number of observations required for a population census to be included in the spatial density estimation (number of deer seen) or for a deer in a given year to be included in analyses (number of observations of that deer across population censuses).

For population density, the number of identified deer observed within a census ranged from 1 to 351 with a mean of 205. For each census with at least 250 deer observed, we estimated the 2-D KDE from the full census data, and then subsampled from 5-250 data points in increments of 5, estimating a 2D KDE for each subset. We recorded the correlation between the full census data density KDE and each subset data KDE across the pixels of the KDE (fitted to a shapefile, see Methods). We repeated this for the 369 censuses that recorded more than 250 deer. For each subset of datapoints we took the mean and 95% quantile range of the correlation coefficients across censuses.

We followed the same process for the number of observations of each deer within a year. We did so at two thresholds for minimum number of observations. The number of observations of an individual within a year ranges from 1 to 46, with a mean of 19. First, we used individual annual-level census data at a threshold of 40 observations (n=205). Second, we randomly sampled 1000 individual:years from the 7428 with at least 20 observations. We repeated this at the lower threshold in case the higher cut off was biased the sample to deer with home ranges more central to the study area.

As expected, the strength of the correlation increased with the number of observations (Figure S2,3). For population density, the variance was much higher, and mean lower, beneath 25 samples. The mean was very high with low uncertainty beyond 50 observations, which we continued to use in our main analyses. This cut off also seemed sensible based on knowledge of the field data collection, as seeing any fewer is likely the result of bad weather, biasing how many can be seen.

For the observations per individual within a year, the mean correlations were high throughout (Figure S3). The lower quantile was greater than 0.8 from 10 observations upwards, which we used as our cut-off in the main analyses. We also reran our main models using a cut-off of 5 and 15 observations to consider whether the threshold chosen influenced our conclusions. The sample sizes for each threshold were 2987, 2876 and 2717 for 5, 10 and 15 observations respectively.

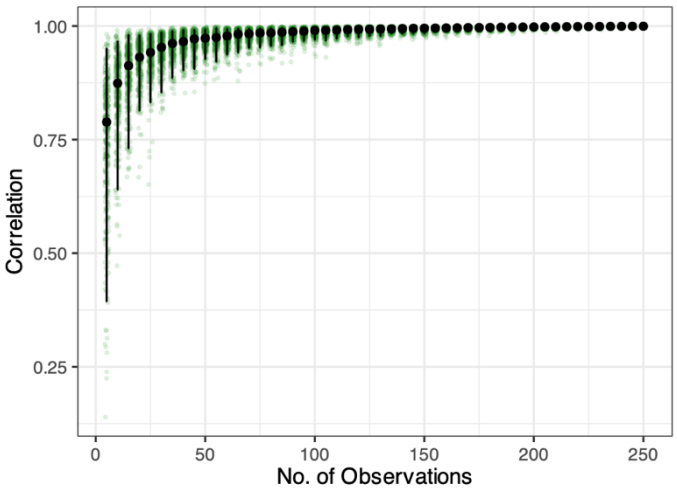


Figure S2: Correlation between KDEs estimated using reduced or full datasets from each population census. Number of observations shows the number of data points each census was reduced to.

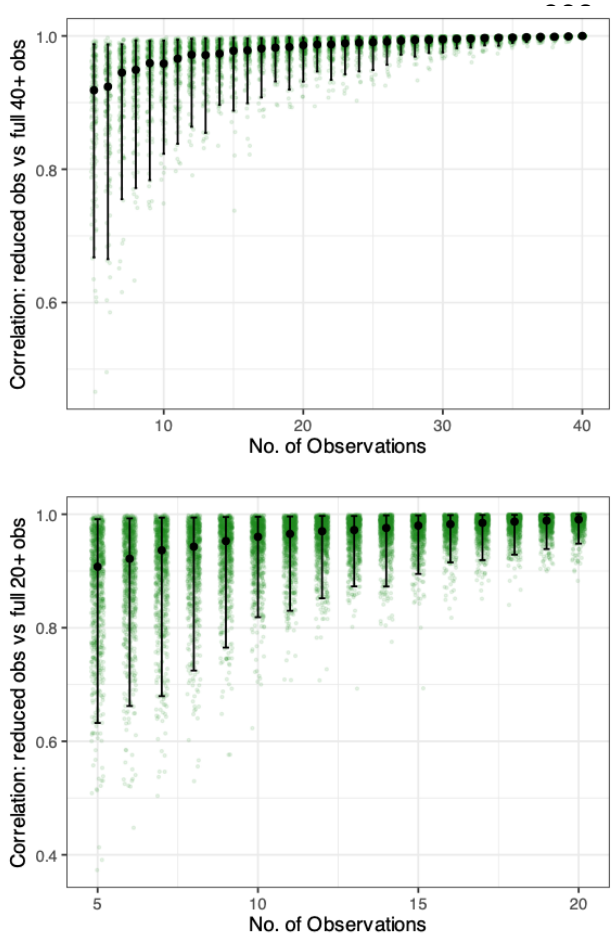
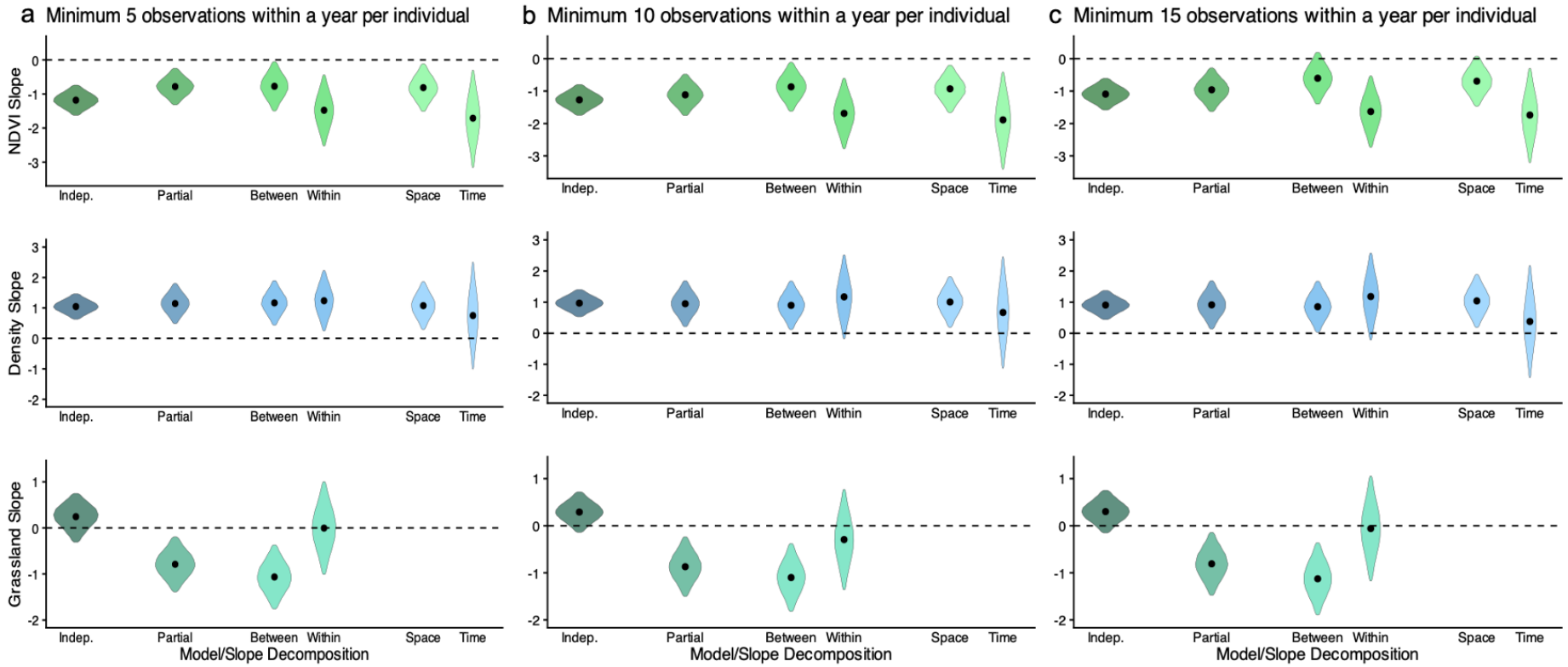


Figure S3: Correlation between KDEs estimated using reduced or full datasets from each individual in each year within the population censuses. Two thresholds were trialled: a) 40 and b) 20, as more observations are likely ideal but the higher threshold may limit the spatial distribution of home ranges included. Number of observations shows the number of data points each individual:year was reduced to.

Comparing models of calving date using different thresholds of inclusion

In general, the posterior distributions of slopes coefficients for the effects of local NDVI, density and access to grassland on calving dates were very similar across the different observation thresholds tested (Figure S4). The interpretation of our results would be consistent at any threshold.



906

907 Figure S4: Model slope coefficients for the effects of NDVI, density and access to grassland on calving dates in red deer. The data frame has

908 been restricted by different thresholds of observations; with a minimum number of observations within a year of a) 5, b) 10 as used in our main

909 analyses or c) 15.

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