scientific reports

OPEN

Timing of rainfall influences juvenile and yearling mass of a long-lived herbivore in a semiarid environment

Miranda L. Hopper[1]✉, **Bryan D. Spencer**[1], **Randy W. DeYoung**[1], **Aaron M. Foley**[1], **J. Alfonso Ortega-Santos**[1], **Timothy E. Fulbright**[1], **David G. Hewitt**[1], **Landon R. Schofield**[2], **Tyler A. Campbell**[2] & **Michael J. Cherry**[1]

Resource availability is a primary factor predicting population performance. Synchrony between resource availability and consumer requirements plays a critical role in reproduction, and mismatches in the timing of resource availability and consumer requirements can have negative implications for reproductive success. Our objective was to determine when mass of juvenile and yearling white-tailed deer (*Odocoileus virginianus*) in semiarid rangelands is most negatively affected by limited forage availability. Thus, we determined the biological period when rainfall, a primary driver of resource availability, was most predictive of juvenile and yearling mass. Over 12 years, we captured 1,123 juveniles and yearlings across five distinct populations. We linked georeferenced capture records to rainfall data from biological seasons hypothesized to affect juvenile and yearling mass. We found that rainfall during the early growing season exhibited the strongest effect on mass. The resource pulse associated with early growing season rainfall is likely used to fuel fetal development during the critical final trimester of gestation. As environmental change continues to exacerbate the potential for mismatches in resource availability and consumer requirements to occur, it is important to identify when limited forage availability may most negatively affect reproduction to inform species conservation and support long-term sustainability.

Keywords Climate change, Drought, Environmental stochasticity, *Odocoileus virginianus*, Phenological mismatch, White-tailed deer

Resource availability exerts a strong influence on population performance[1–3]. The match-mismatch hypothesis (MMH) suggests variable recruitment of a population is a product of energetic demands relative to availability of the resource at the immediate lower trophic level[4]. Animals often reproduce during peak resource abundance to ensure the energetic requirements associated with reproduction are met[5,6]. However, in the face of dynamic environmental conditions, including climate change, shifts in resource availability patterns can result in phenological mismatches between animals and their environment, as climate change is predicted to induce different responses across trophic levels[7]. These mismatches occur when the timing of resource availability no longer aligns with the peak requirements of consumers[8]. Such phenological mismatches have become a subject of growing concern due to their potential impacts on population dynamics and ecological interactions[9–11].

In terrestrial environments, vegetation onset and growth are determined by a combination of biotic and abiotic factors, such as temperature and precipitation. Conversely, reproduction of many herbivores is cued by seasonal changes in the photoperiod, which remains constant from year to year[12,13]. The temporal variation in the onset of vegetation growth and contrasting stability of photoperiodism exacerbates the potential for a mismatch, and the degree to which animals will be affected depends on their ability to adapt their response to photoperiod to variable resource availability[14–16]. Importantly, though some adaptation is possible at localized scales, environmental change often occurs unpredictably and at a pace that is too rapid to allow sufficient time for adaptation. For example, in a study of two populations of roe deer (*Capreolus capreolus*), increasingly early springs led to declines in recruitment, and ultimately, a reduction in population growth rate as roe deer were unable to track changes in vegetation phenology[17]. Additionally, in many cervid species (Family *Cervidae*),

[1]Caesar Kleberg Wildlife Research Institute, Kingsville, TX 78363, USA. [2]East Foundation, San Antonio, TX 78216, USA. ✉email: Miranda.hopper@students.tamuk.edu

breeding occurs several months before the peak energetic demands of late gestation and lactation, leaving individuals with considerable uncertainty at conception about whether resources will be sufficient when those demands are greatest. Therefore, phenological mismatches become more likely when timing of vegetation growth shifts and individuals are forced to make the decision to reproduce without reliable knowledge of future resource availability.

Changes in weather patterns alter plant phenology and resource availability for herbivores[18,19]. Rainfall affects the timing, abundance, and quality of nutritional resources[20–22], which has important consequences for ungulates. The timing and duration of vegetation growth influences numerous aspects of ungulate life history, including migration[23], timing of reproduction[5,24,25], maternal investment[25], population demography[26], offspring body mass, and female reproductive success[27–29]. Body mass is a critical component of fitness as it is related to probability of survival and time to primiparity, and thus, lifetime reproductive potential[30,31]. Therefore, it is important to understand the long-term fitness consequences of enduring mismatches in early life.

Semiarid environments, characterized by extreme temperatures, highly variable rainfall, and frequent drought, are distributed across the globe. Species in these environments have adapted to cope with unpredictable resource availability and can provide valuable insights into the responses of their counterparts in other regions to changing environmental conditions. White-tailed deer (*Odocoileus virginianus*), a highly adaptable large herbivore, inhabit a wide range of climatic regions, from the boreal forests of Canada to the tropical forests of Bolivia. In semiarid environments, white-tailed deer (hereafter, deer) have experienced extreme variability in weather and nutritional resources. In these stochastic systems, deer nutrition is primarily determined by resource availability driven by variation in rainfall[32–34].

Climate-induced phenological mismatches are of growing concern because of the implications they have for long-term population performance and sustainability. The MMH offers a simple framework for studying phenological mismatches. To evaluate the potential for mismatches in resource availability to influence population performance, it is essential to first understand what constitutes a match[35]. Our objective was to determine the timing of resource availability that is most impactful on juvenile and yearling mass to reveal when mass is most negatively affected by limited forage availability in a highly dynamic system. Deer in semiarid environments serve as an ideal model system for several reasons. First, deer in semiarid environments have adapted to an environment that provides insight into future conditions expected across the wider geographic range of the species, as other systems are projected to become more variable, resembling semiarid conditions under future climate change[36]. Second, rainfall is the primary driver behind resource availability for deer in this environment[33,34]. Lastly, young individuals are more sensitive to environmental changes than adults[37], making them an early indicator of the effects of changing conditions. Thus, we defined biological seasons based on a priori hypotheses related to consumer and autotroph requirements. We then determined the biological period in which rainfall was most predictive of juvenile and yearling body mass. We hypothesized that juvenile and yearling mass would be most influenced by limited forage availability during periods of peak consumer requirements. Thus, we predicted that juvenile and yearling mass would be most influenced by rainfall occurring during seasons that would affect resource availability as energetic requirements associated with reproduction increased. We considered seasons that were the most energetically demanding for reproductive females as they need access to resources to maximize reproductive success and investment in their young. We also considered important plant growing seasons when autotroph requirements are highest and rainfall is important for establishing plant productivity[38,39]. We confronted this hypothesis with data generated from the capture of over 1,100 juvenile and yearling deer from five populations during 12 years across a broad geographic extent.

Results

Rainfall was highly variable from 2011 to 2022 (Fig. 1). Overall, average daily rainfall varied from a minimum of 0 cm in 2011 during the early growing season (April 1st -30th) to a maximum of 0.65 cm in 2021 during the third trimester of gestation (May 6th -July 12th). Daily rainfall typically was greatest during the third trimester of gestation with an average of 0.29 cm (SD = 0.17 cm) of rainfall per day (Supplementary Table S1). Daily rainfall was lowest during the early growing season with an average of 0.13 cm (SD = 0.12 cm) of rainfall per day (Supplementary Table S1).

From 2011 to 2022, we captured 514 juveniles (males = 231, females = 283) and 609 yearlings (males = 321, females = 288) across the five populations (Supplementary Tables S2 & S3). Of the 609 yearlings, 50 were also captured as juveniles. Juvenile body mass averaged 19.7 kg (SD = 4.09 kg), with males ($\bar{X}$ = 20.4 kg; SD = 4.21 kg) being 6.4% larger than females ($\bar{X}$ = 19.1 kg; SD = 3.90 kg). Body mass for yearlings averaged 36.6 kg (SD = 6.27 kg). Yearling males ($\bar{X}$ = 38.7 kg; SD = 6.59 kg) were 11.6% larger than females ($\bar{X}$ = 34.2 kg; SD = 4.90 kg).

Rainfall during the early growing season had a stronger effect on juvenile mass than rainfall in any other season. Our most supported model predicting juvenile body mass included sex and early growing season rainfall (Table 1; Fig. 2). Specifically, we found that for every 10 cm increase in cumulative early growing season rainfall, juvenile body mass increased by 2.3 kg ($\beta = 0.023$; SE ± 0.008; $P < 0.01$; Table 2). We found no support for any other model (Table 1).

The most supported model for yearling body mass included sex, current-year early growing season rainfall, and previous-year early growing season rainfall (Table 1; Fig. 3). Model results indicate that for every 10 cm increase in current-year and previous-year early growing season rainfall, yearling body mass increased by 4.4 kg ($\beta = 0.044$; SE ± 0.015; $P < 0.01$; Table 2) and 3.0 kg ($\beta = 0.030$; SE ± 0.013; $P = 0.03$; Table 2), respectively. As with juveniles, we found no support for any other model predicting yearling body mass (Table 1).

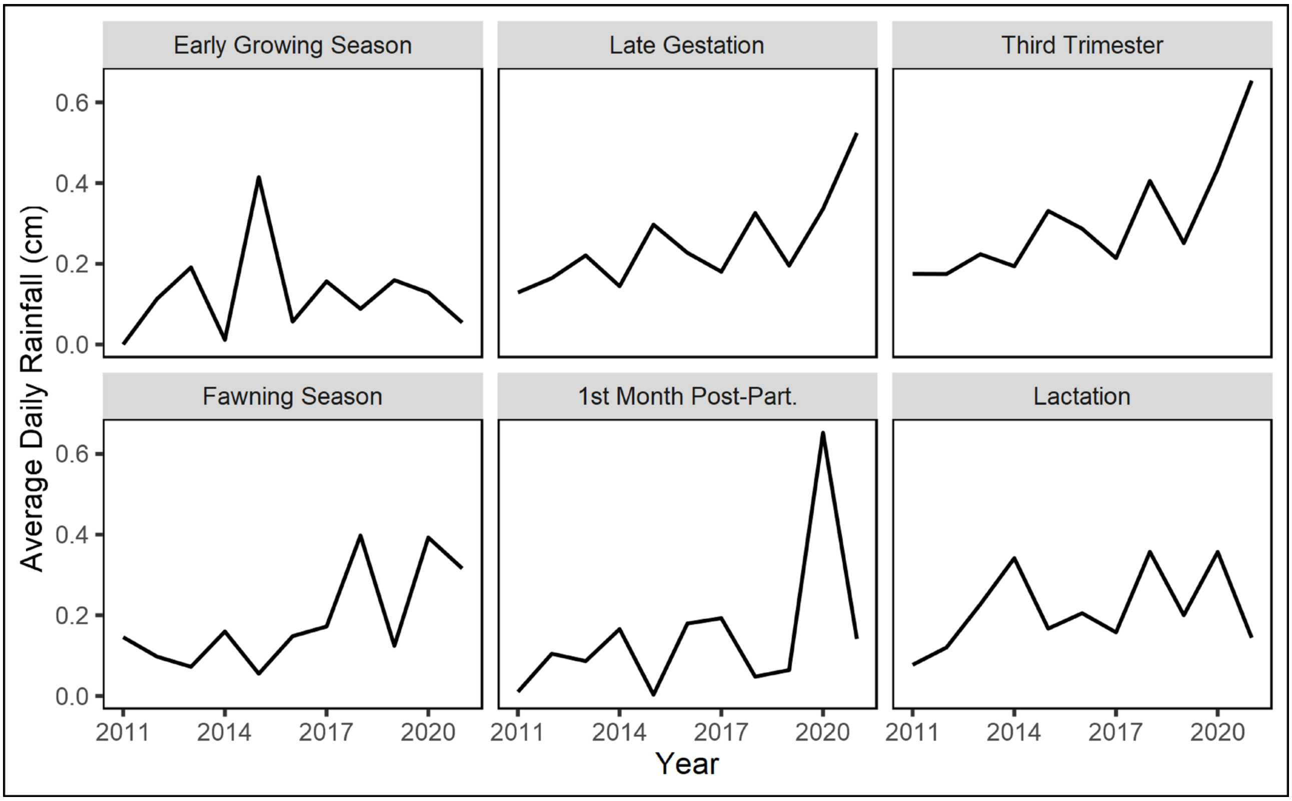

Fig. 1. Distribution of daily rainfall (cm) occurring during six biological periods in which rainfall is hypothesized to influence body mass of juvenile and yearling white-tailed deer in autumn from 2011 to 2022 in South Texas, USA: early growing season (April 1st -April 30th), late gestation (April 3rd -July 12th), third trimester (May 6th -July 12th), fawning season (June 16th -August 20th), first month post-parturition (July 12th -August 12th), and lactation (July 12th -October 20th).

	Candidate models[1]	k	AIC	ΔAIC	w_i
Juveniles					
1	Early growing season + Sex	6	2860.299	0.000	0.682
2	Late gestation + Sex	6	2863.473	3.174	0.139
3	3rd trimester + Sex	6	2865.155	4.856	0.060
4	1st month post-parturition + Sex	6	2865.897	5.598	0.041
5	Lactation + Sex	6	2865.938	5.639	0.041
6	Fawning season + Sex	6	2866.152	5.853	0.037
7	Null	4	2876.323	16.024	0.000
Yearlings					
1	Previous early growing season + Early growing season + Sex	7	3791.065	0.000	0.791
2	Early growing season + Sex	6	3794.113	3.048	0.172
3	Previous early growing season + Sex	6	3797.195	6.130	0.037
4	Null	4	3892.562	101.50	0.000

Table 1. Results from modeling procedure examining the effect of seasonal rainfall on body mass of juvenile and yearling white-tailed deer in South Texas, USA from 2011 to 2022. [1] Dates of seasons were delineated as: Late Gestation (April 3rd -July 12th), 3rd Trimester (May 6th -July 12th), Fawning Season (June 16th -August 20th), 1st Month Post-Parturition (July 12th -August 12th), Lactation (July 12th -October 20th), and Early Growing Season (April 1st -April 30th).

Discussion

We investigated the influence of rainfall during different seasons on the mass of juvenile and yearling deer in a semiarid system. Our findings provided support for our hypothesis that juvenile and yearling mass would be most affected by limited forage availability during periods of peak consumer requirements, as rainfall during

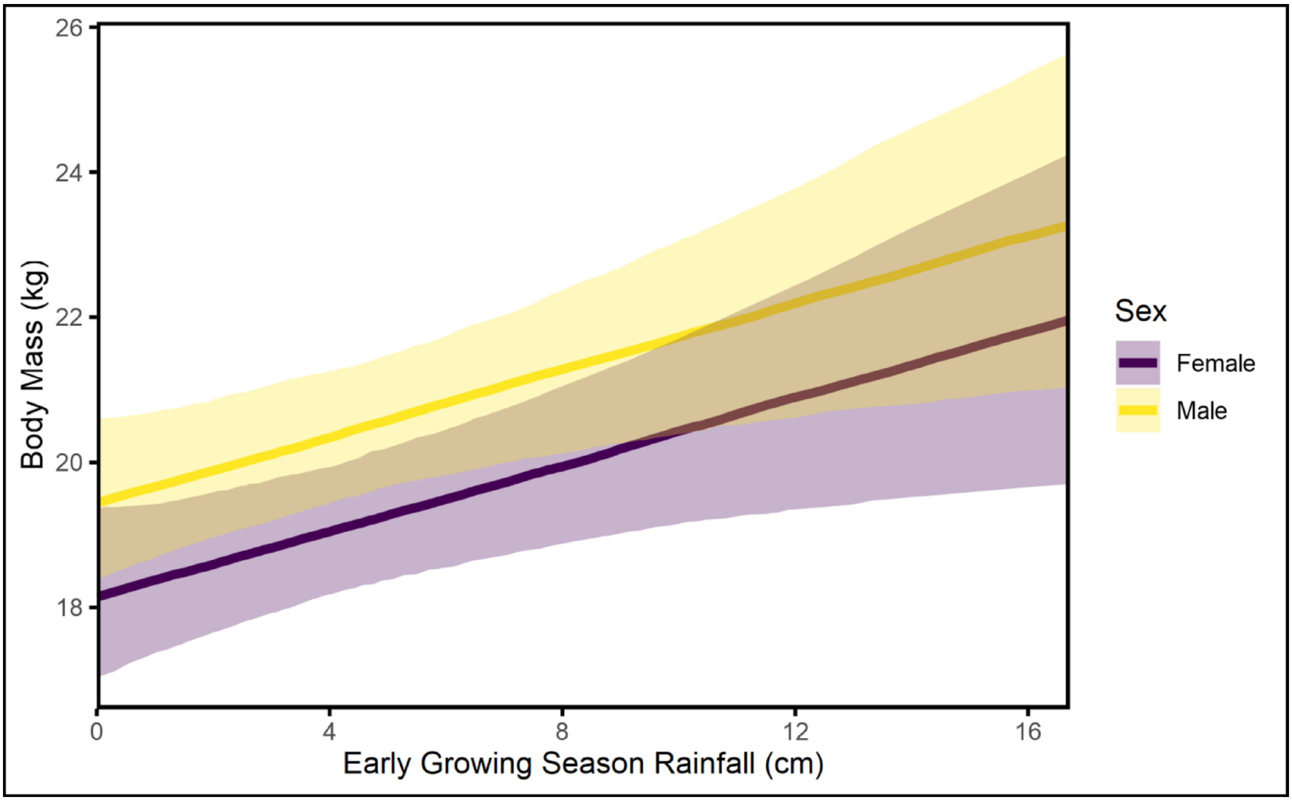

Fig. 2. The effect of early growing season rainfall (cm) on the body mass (kg) of 514 white-tailed deer juveniles captured in South Texas, USA from 2011 to 2022. Confidence bands represent a 95% confidence level.

Models	Beta estimate	SE
Juveniles		
Early growing season + Sex		
Early growing season	0.23	0.09
Sex	1.28	0.34
Yearlings		
Early growing season + Previous early growing season + Sex		
Early growing season	0.44	0.15
Previous early growing season	0.30	0.13
Sex	4.41	0.43

Table 2. Results from modeling procedure examining the effect of rainfall (cm) on body mass (kg) of juvenile and yearling white-tailed deer in South Texas, USA from 2011 to 2022. Beta estimates and standard errors for all terms of the most supported models are reported.

the early growing season (April) exhibited the strongest effect on the body mass of juveniles and yearlings. Additionally, we observed prolonged effects of early growing season rainfall, in that rainfall during the early growing season of the birth year influenced yearling body mass one year later. This indicates that early growing season rain corresponds to a match scenario in our study system. The match scenario is the period when resource availability is most important to maximize population performance. In our system, the resource pulse associated with rainfall was likely used to directly fuel fetal development during the critical period of the final trimester of gestation from May to June due to lag effects on vegetation and soil moisture. Our study provides support for the MMH as variation in rainfall during the match period (early growing season) influenced body mass through its effect on resource availability (Fig. 4). Moreover, our results suggest that the MMH can be expanded to include metrics of population performance beyond recruitment[4], such as body mass of juveniles and yearlings.

We observed that early growing season rainfall had the strongest effect on juvenile and yearling mass. Previous research has shown that rainfall in the spring positively affects juvenile white-tailed deer survival and body weight[40,41], which has been observed in other ungulate species, like chamois (*Rupicapra rupicapra*)[42]

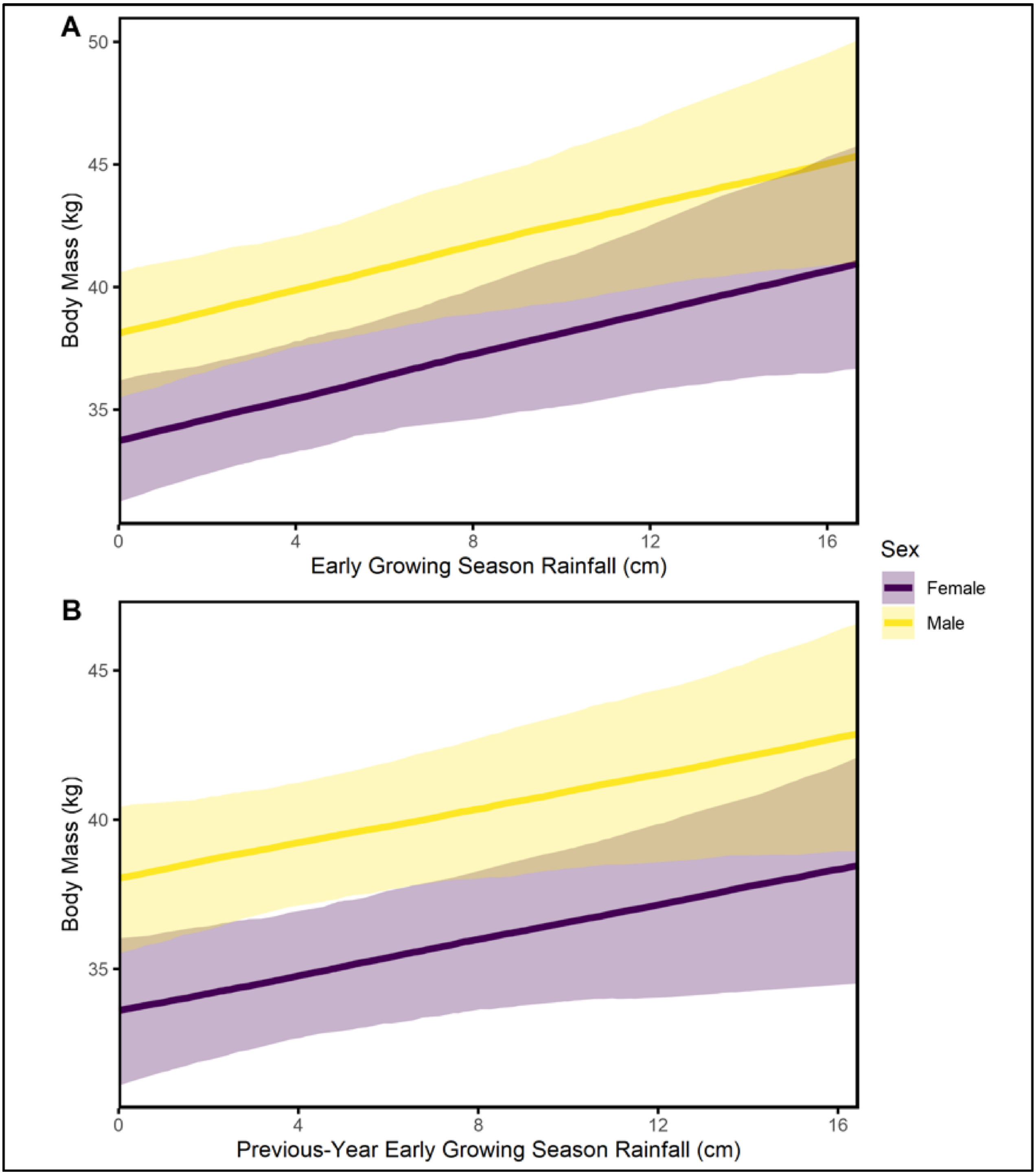

Fig. 3. The effect of birth-year (**B**) and current-year (**A**) early growing season rainfall (cm) on the body mass (kg) of 609 white-tailed deer yearlings captured in South Texas, USA from 2011 to 2022. Confidence bands represent a 95% confidence level.

and roe deer[43]. Early growing season rain influences the available forage for maternal females, and thus their nutritional condition, as they enter the late stages of gestation and lactation. Access to these resources improves reproductive output and maternal investment in offspring[44–46], and improvements in quantity and quality of maternal resources during pregnancy have been shown to improve juvenile survival of deer species[47,48].

Late spring and summer mark a nutritionally stressful period for yearlings. At this stage, yearlings are prioritizing growth over reproduction as most female deer in this region will not reach primiparity until 2.5 years old[49]. Accumulation of body mass is important for future breeding and survival, as heavier individuals tend to have a higher probability of survival[30]; thus, resource availability is increasingly important for yearlings.

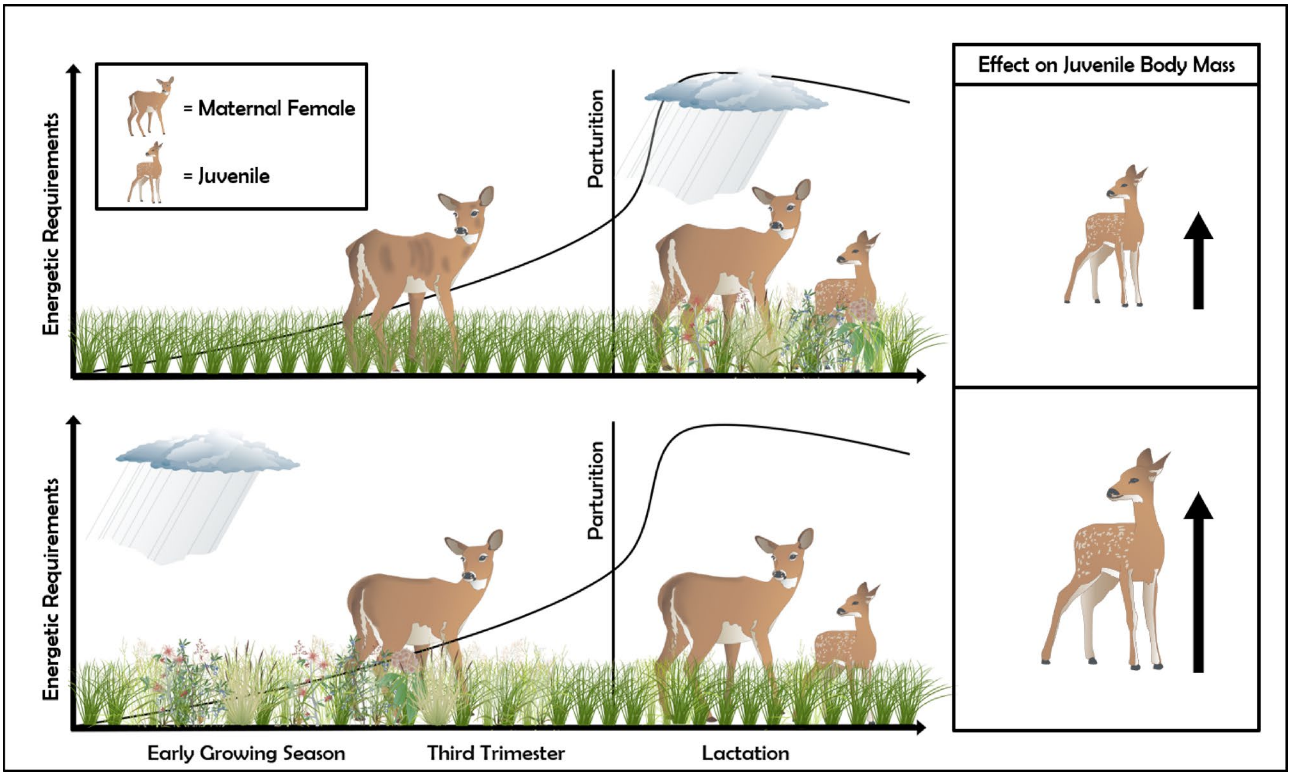

Fig. 4. Conceptual figure illustrating the observed effect of rainfall on body mass of juvenile white-tailed deer when rainfall is received during lactation versus the early growing season. When rainfall occurs during lactation, maternal females use forage resources to support lactation, and we observe an increase in juvenile body mass. However, when rainfall occurs during the early growing season, maternal females use forage resources to support gestation and improve their body condition ahead of lactation, resulting in a greater increase in juvenile body mass.

We found evidence of lasting effects of early growing season rainfall on body mass in the year-of-birth over one year later. This suggests that limitations in early growing season rainfall in the year-of-birth had prolonged effects on yearling mass. This is consistent with several studies which have found that early life conditions, including conditions during gestation and post-parturition, have permanent implications for body mass, with those experiencing resource shortages in their early life being smaller into adulthood[50–54]. Conversely, other studies have observed that individuals who experience resource limitations in their first year are able to recover in subsequent years[31,55]. Our study did not include adults and therefore did not further our understanding of permanent effects of early life conditions. Previous research has revealed that variation in adult body mass and skeletal size on our study areas are driven more by fixed resources, including soil type and woody plant community, than rainfall or forb availability[56]. This suggests that compensatory growth occurs in our region, though we do not have data to fully understand this mechanism. Regardless, our results supported by data from 609 yearlings provide clear evidence that conditions during gestation have long-lasting effects on mass that extend to the yearling age class.

Using data from five populations and daily rainfall data recorded over 12 years, we found early growing season rainfall is an important driver of juvenile and yearling body mass, and early growing season rainfall in the birth-year has prolonged implications for yearling mass. Our findings provide mechanistic insight to how the environmental conditions an individual experiences during gestation affect future survival and lifetime reproductive success[30,57]. Thus, early growing season rainfall constitutes a match scenario in our study system where resource availability has the greatest effect on juvenile and yearling mass. Our results highlight that what should be considered a match scenario is not necessarily during lactation immediately post-parturition – the period when energetic requirements of the consumer are at their greatest peak[58]. Therefore, when assessing the applicability of the MMH within a system, one must first identify the match period when limited forage availability is most impactful to metrics of population performance, such as juvenile and yearling body mass. Rainfall during the early growing season promotes resource availability in the late spring when deer are entering the final trimester of gestation, a period marked by increased energetic demands, and subsequently provides critical resources to fuel fetal development and increase juvenile body mass several months post-parturition. As climate change continues to exacerbate environmental stochasticity and unpredictability in resources within semiarid systems, an understanding of how resource availability influences population performance is critical to sustainable species management.

Methods

Study area

We conducted research on five sites within South Texas, USA: San Antonio Viejo (SAV) Ranch (60,752 ha within Jim Hogg and Starr counties), divided into SAV-North and SAV-South, Buena Vista Ranch (6,113 ha in Jim Hogg County), Santa Rosa Ranch (7,544 ha in Kenedy County), and El Sauz Ranch (10,984 ha in Kenedy and Willacy counties). All study sites were located in the Coastal Sand Sheet ecoregion. The Coastal Sand Sheet was characterized by sandy soils, resulting from colluvial soil formations created by Gulf Coast winds. Additionally, this semiarid environment was prone to extreme temperatures and highly variable rainfall (Fig. 1). Temperatures averaged 14°C in January to 32°C in August (30-year averages) and often exceeded 38°C in the summer[59]. Rainfall was highly variable both spatially and temporally across the region. Across the study area, observed rainfall during the study period varied from as low as an average of 27 cm in 2011 to as high as 78 cm in 2021[59]. Additionally, there existed an environmental gradient across the region with sandier, less productive soils and higher rainfall in the east and more productive soils but less rainfall in the west. Annual rainfall in the east, along the Gulf Coast, averaged 94 cm, and in the west, averaged 49 cm (30-year average; Fig. 5)[59]. Plant communities were dominated by honey mesquite (*Neltuma glandulosa*), live oak (*Quercus virginiana*), huisache (*Vachellia farnesiana*), brasil (*Condalia hookeri*), whitebrush (*Aloysia gratissima*), and prickly pear cacti (*Opuntia engelmannii*). Herbaceous plant communities consisted of species including woolly croton (*Croton capitatus*), seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), purple threeawn (*Aristida purpurea*), and spotted beebalm (*Monarda punctata*).

South Texas experiences hot and humid summers and mild, short winters. Average monthly rainfall is lowest during winter and highest during the late spring (May-June) and fall (September). Vegetation communities are primarily driven by variation in rainfall patterns and limited by drought conditions[60,61]. South Texas rarely receives its "average" rainfall but rather most years are characterized as either receiving above-average or below-average rainfall. Many forbs are annual and only occur in years with sufficient rainfall[61]. Forbs in the region are primarily cool-season plants that grow in the spring but senesce by early summer due to warming temperatures and limited moisture[61,62]. During summer, mast-producing plants, like prickly pear cacti and honey mesquite are readily available forages even under drought conditions. Additionally, browse is a continuously available forage, though many of the woody plant species in our study area are drought-deciduous[60–62]. During non-drought years, white-tailed deer diets consist of forbs in spring, mast in summer, and browse in autumn and winter[61,62].

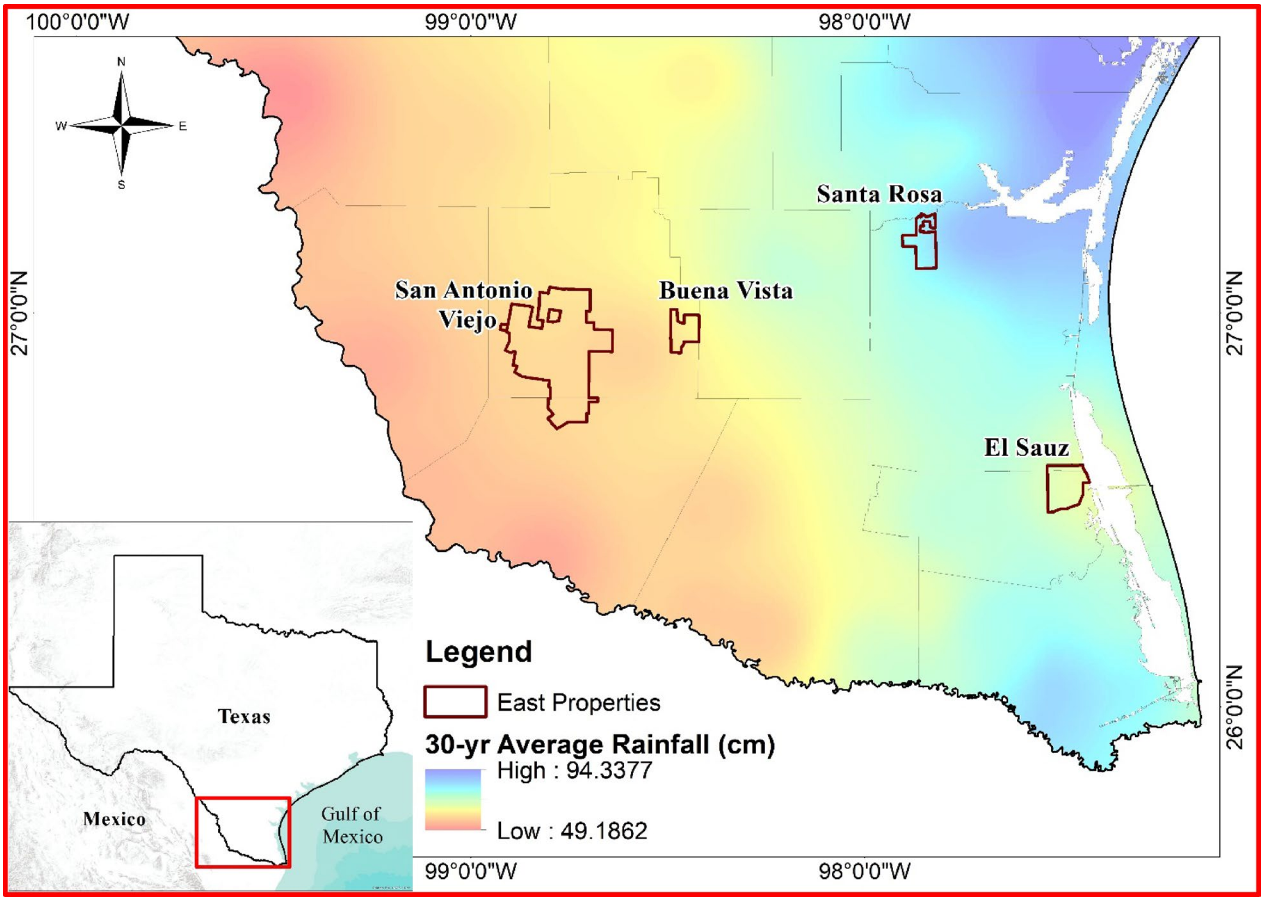

Fig. 5. Map depicting the distribution of 30-year average rainfall (cm) across South Texas, USA. Also shown are properties owned by the East Foundation where captures of white-tailed deer took place from 2011 to 2022.

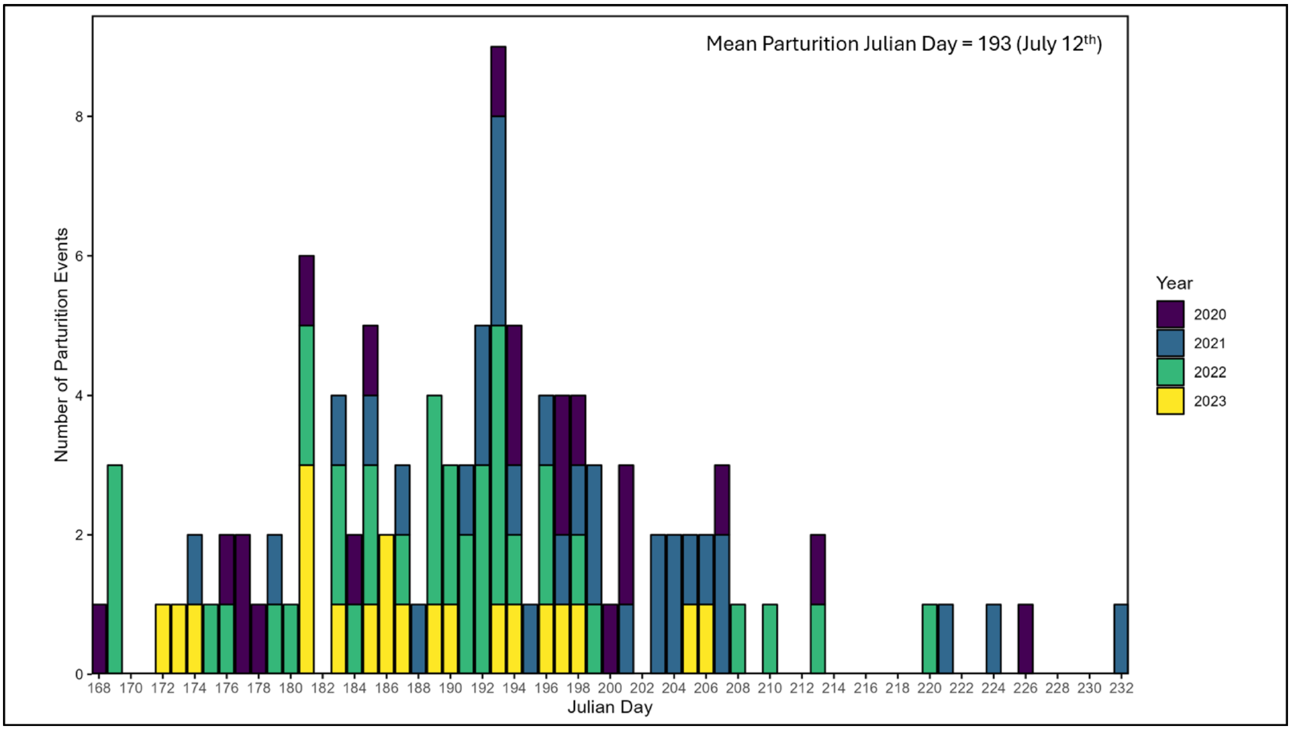

Fig. 6. Figure showing the distribution of parturition dates of white-tailed deer observed during 2020 (*n* = 20), 2021 (*n* = 31), 2022 (*n* = 38), and 2023 (*n* = 20) at the East Foundation's San Antonio Viejo Ranch in South Texas, USA.

Conversely, in drought years, deer consume diets that are low in digestible protein and consist primarily of flowers, mast, and browse[63]. These lower-quality diets are generally adequate to meet protein requirements to support survival of adult deer but not survival and optimal growth of juveniles[63]. However, deer maintain diets with high levels of metabolizable energy even in drought years, particularly during autumn and winter[63]. During these seasons, deer consume diets with excess energy which allows deer to restore body condition and build energetic stores to support gestation and lactation during spring and summer[63].

The research sites were working cattle ranches owned by the East Foundation, an agricultural research organization. Land management practices included cattle (*Bos taurus*) grazing, prescribed fire, and brush management targeted at cattle production and wildlife habitat management. Within our study sites, deer were not hunted or supplementally fed. Primary predators in the study area included coyotes (*Canis latrans*) and bobcats (*Lynx rufus*)[64].

Data collection

From 2011 to 2022, we captured deer via aerial net-gunning[65] during October and November of each year. Capture areas were strategically selected to allow us to efficiently maximize accessibility and property coverage during designated flight time, while minimizing the distance required for transport of deer from their capture location to the central processing station. Generally, we repeatedly sampled the same capture areas each year of the study. To achieve randomization in the capture process, we instructed helicopter pilots to pursue the first individual spotted, regardless of group size, age, sex, or body size. We recorded the capture location using a handheld GPS unit and restrained, blindfolded, and transported deer to a central processing station. We recorded body mass to the nearest 0.45 kg and estimated age using tooth replacement and wear[66]. We categorized individuals as juveniles (3–4 months old), yearlings (15–16 months old), or adults (≥ 2 years old). We identified juveniles as those with fewer than six erupted teeth. Yearlings were identified as those with six fully erupted teeth and with three cusps present on the third premolar. Adults were identified as all individuals with six fully erupted teeth and a bicuspid third premolar. We marked each individual with uniquely numbered ear tags then released them onsite.

We determined the timing of reproductive seasons by capturing adult female deer on SAV-N using aerial net-gunning in March 2020 (*n* = 20), 2021 (*n* = 31), 2022 (*n* = 38), and 2023 (*n* = 20). We used these data to determine the timing of reproductive seasons, but not to assess juvenile and yearling mass. We determined pregnancy status using ultrasonography and, if pregnant, equipped females with vaginal implant transmitters (VIT; Advanced Telemetry Systems, Isanti, MN, United States). We programmed VITs to send a very high frequency (VHF) signal once the VIT reached a temperature threshold below 30°C, indicating expulsion prior to parturition. We compiled all observed parturition dates across the four years of the study into one dataset (Fig. 6). We then delineated the fawning season as the period between the earliest recorded parturition date (June 16th) and the latest recorded parturition date (August 20th). We calculated the average parturition date across all four years (July 12th) and used this as a starting point for delineating the other reproductive seasons. Specifically, we considered July 12th through August 12th to be the first-month post-parturition. We assumed a lactation period of 100 days after which most juveniles are weaned and functional ruminants[67,68]. Thus, we identified July 12th through October 20th as the period of lactation. Additionally, the mean period of gestation for white-tailed deer is 200 days[69]. We identified late gestation as the latter half of gestation and subtracted 100 days from the mean parturition date, thus classifying late gestation as April 3rd through July 12th. Lastly, we considered the third trimester to be the final 67 days of gestation. Therefore, we subtracted 67 days from the mean parturition date, identifying the third trimester as May 6th through July 12th. Previous research in the study area suggested breeding activity varied less than two weeks across study sites[70], and therefore, we used these standardized dates defined by the VIT data to delineate reproductive seasons across sites.

All experimental protocols were approved by the Texas A&M University-Kingsville Institutional Animal Care and Use Committee (permit number: 2020-10-19). All methods were carried out in accordance with relevant guidelines and regulations, including the guidelines of the American Society of Mammalogists (Sikes and the Animal Care and Use Committee, 2016). Permission to conduct fieldwork on participating ranches was granted by the East Foundation and Texas Parks and Wildlife Department (permit number: SPR-1021-170).

Statistical analysis

To assess juvenile and yearling mass, we used body mass measurements of captured juveniles and yearlings. We considered heavier individuals to be of higher quality because heavier individuals often have a higher probability of survival and achieve primiparity faster, therefore promoting lifetime reproductive success[30,31].

We identified six time periods during which we hypothesized rainfall would have the greatest effect on body mass of juveniles and yearlings. The six periods included the early growing season (April 1st – April 30th), late gestation (April 3rd – July 12th), third trimester (May 6th – July 12th), fawning season (June 16th – August 20th), first-month post-parturition (July 12th – August 12th), and lactation (July 12th – October 20th). We chose April as a month representing the early growing season, because this month marks the beginning of an important plant growth period in this study system and can affect forage production during the late spring when deer are approaching the final trimester of gestation[71]. We obtained estimates of cumulative daily rainfall from 2011 to 2022 for each of the five sites at 4-km resolution[59]. We extracted values of daily rainfall to every capture location then calculated the sum of daily rainfall values to obtain cumulative rainfall experienced by each individual during each of the six time periods.

To determine the effect of rainfall on body mass of juveniles and yearlings and to identify the season most predictive of body mass, we used linear mixed-effects models. In these models, we considered body mass as the response variable and examined the influence of rainfall during a specific season as the explanatory variable. We included year (n = 12) and capture site (n = 5) as random effects on the intercept. We also included sex as a covariate in all models to account for sex-specific differences in body mass. We fit seven models predicting juvenile mass, including a null model (Table 1). Each model included sex and cumulative rainfall during one of the six biological seasons (Table 1). To identify the top model, and the season in which rainfall had the greatest effect on juvenile mass, we evaluated models using Akaike Information Criterion (AIC)[72]. We identified the model with the lowest AIC score as the most supported model, and we identified competing models using a ΔAIC < 2[73]. After identifying the top model, we evaluated covariate estimates using the Satterthwaite method to approximate degrees of freedom and t-tests to determine statistical significance ($P \leq 0.05$)[74].

For yearlings, we fit four models to predict yearling body mass, including a null model (Table 1). We included rainfall during the early growing season of the capture year in the models. Additionally, we were interested in the effect of rainfall in the year of birth on yearling mass. Therefore, we first identified the top model for juveniles and included the identified season as a birth-year effect in the yearling model. We used AIC to determine the best yearling model and season of rainfall which should be considered a match scenario. We considered the model with the lowest AIC score the most parsimonious model, and covariates with $P \leq 0.05$ were deemed statistically significant. We performed analyses in R version 4.3.1 using the 'lme4' package (version 1.1.34)[75].

Data availability

The data used in this manuscript is provided via Zenodo at the following link: https://doi.org/10.5281/zenodo.12611417.

Received: 30 June 2025; Accepted: 16 February 2026

References

1. Blomberg, E. J., Sedinger, J. S., Gibson, D., Coates, P. S. & Casazza, M. L. Carryover Effects and Climatic Conditions Influence the Postfledging Survival of Greater Sage-grouse. *Ecol. Evol.* **4**, 4488–4499 (2014).
2. Lopp, J. & Sammul, M. The Impact of Timing of Resource Availability on Clonal Propagation of Species with Different Growth Forms. *Folia Geobot.* **52**, 411–422 (2017).
3. Mazzamuto, M. V. et al. Timing of Resource Availability Drives Divergent Social Systems and Home Range Dynamics in Ecologically Similar Tree Squirrels. *Front. Ecol. Evol.* **8**, 174 (2020).
4. Durant, J. M., Hjermann, D. Ø., Ottersen, G. & Stenseth, N. C. Climate and the Match or Mismatch Between Predator Requirements and Resource Availability. *Clim. Res.* **33**, 271–283 (2007).
5. Neumann, W. et al. Divergence in Parturition Timing and Vegetation Onset in a Large Herbivore—Differences Along a Latitudinal Gradient. *Biol. Lett.* **16**, 20200044 (2020).
6. Peláez, M., Gaillard, J. M., Bollmann, K., Heurich, M. & Rehnus, M. Large-scale Variation in Birth Timing and Synchrony of a Large Herbivore Along the Latitudinal and Altitudinal Gradients. *J. Anim. Ecol.* **89**, 1906–1917 (2020).

7. Visser, M. E. & Gienapp, P. Evolutionary and Demographic Consequences of Phenological Mismatches. *Nat. Ecol. Evol.* **3**, 879–885 (2019).
8. Kerby, J. T., Wilmers, C. C., & Post, E. Climate Change Phenology, and the Nature of Consumer–resource Interactions: Advancing the Match/mismatch Hypothesis. in *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives* (eds. Ohgushi, T., Schmitz, O. & Holt, R. D.) 508–525. (Cambridge University Press, 2012).
9. Post, E. & Forchhammer, M. C. Climate Change Reduces Reproductive Success of an Arctic Herbivore through Trophic Mismatch. *Philos. Trans. R Soc. B Biol. Sci.* **363**, 2367–2373 (2008).
10. Rehnus, M., Peláez, M. & Bollmann, K. Advancing Plant Phenology Causes an Increasing Trophic Mismatch in an Income Breeder Across a Wide Elevational Range. *Ecosphere* **11**, 03144 (2020).
11. Youngflesh, C. et al. Demographic Consequences of Phenological Asynchrony for North American Songbirds. *Proc. Natl. Acad. Sci.* **120**, 2221961120 (2023).
12. Lincoln, G. A Brief History of Circannual Time. *J. Neuroendocrinol.* **31**, e12694 (2019).
13. Tyler, N. J. C., Gregorini, P., Parker, K. L. & Hazlerigg, D. G. Animal Responses to Environmental Variation: Physiological Mechanisms in Ecological Models of Performance in Deer (Cervidae). *Anim. Prod. Sci.* **60**, 1248–1270 (2020).
14. Apollonio, M. & Chirichella, R. *Deer and Climate Change: Impacts and Perspectives* (Animal Production Science, 2023).
15. Williams, C. T. et al. Seasonal Reproductive Tactics: Annual Timing and the Capital-to-Income Breeder Continuum. *Philos. Trans. R Soc. B Biol. Sci.* **372**, 20160250 (2017).
16. Zerbe, P. et al. Reproductive Seasonality in Captive Wild Ruminants: Implications for Biogeographical Adaptation, Photoperiodic Control, and Life History. *Biol. Rev.* **87**, 965–990 (2012).
17. Gaillard, J. M. et al. How Does Climate Change Influence Demographic Processes of Widespread Species? Lessons from the Comparative Analysis of Contrasted Populations of Roe Deer. *Ecol. Lett.* **16**, 48–57 (2013).
18. Hill, A. P., Nolan, C. J., Hemes, K. S., Cambron, T. W. & Field, C. B. Low-Elevation Conifers in California's Sierra Nevada Are Out of Equilibrium with Climate. *PNAS Nexus*. **2**, 004 (2023).
19. Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669 (2006).
20. Marshal, J. P., Krausman, P. R., & Bleich, V. C. Rainfall, Temperature, and Forage Dynamics Affect Nutritional Quality of Desert Mule Deer Forage. *Rangel. Ecol. Manag.* **58**, 360–365 (2005).
21. Plaisir, C. A., King, W. J., Forsyth, D. M. & Festa-Bianchet, M. Effects of Rainfall, Forage Biomass, and Population Density, on Survival and Growth of Juvenile Kangaroos. *J. Mammal.* **103**, 491–502 (2022).
22. Walter, J. et al. Increased Rainfall Variability Reduces Biomass and Forage Quality of Temperate Grassland Largely Independent of Mowing Frequency. *Agric. Ecosyst. Environ.* **148**, 1–10 (2012).
23. Ortega, A. C., Aikens, E. O., Merkle, J. A., Monteith, K. L. & Kauffman, M. J. Migrating Mule Deer Compensate en Route for Phenological Mismatches. *Nat. Commun.* **14**, 2008. (2023).
24. Aikens, E. O. et al. Migration Distance and Maternal Resource Allocation Determine Timing of Birth in a Large Herbivore. *Ecology* **102**, 03334 (2021).
25. Rachlow, J. L. & Bowyer, R. T. Variability in Maternal Behavior by Dall's Sheep: Environmental Tracking or Adaptive Strategy? *J. Mammal.* **75**, 328–337 (1994).
26. Plard, F. et al. Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. *PLoS Biol.* **12**, 1001828 (2014).
27. Renaud, L. A., Festa-Bianchet, M. & Pelletier, F. Testing the Match–Mismatch Hypothesis in Bighorn Sheep in the Context of Climate Change. *Glob Change Biol.* **28**, 21–32 (2021).
28. Servanty, S., Gaillard, J. M., Toïgo, C., Brandt, S. & Baubet, E. Pulsed Resources and Climate-induced Variation in the Reproductive Traits of Wild Boar under High Hunting Pressure. *J. Anim. Ecol.* **78**, 1278–1290 (2009).
29. Tveraa, T., Stien, A., Bårdsen, B., & Fauchald, P. Population Densities, Vegetation Green-Up, and Plant Productivity: Impacts on Reproductive Success and Juvenile Body Mass in Reindeer. *PloS One*. **8**, 56450 (2013).
30. Cook, J. G. et al. Effects of Summer-Autumn Nutrition and Parturition Date on Reproduction and Survival of Elk. *Wildl. Monogr.* **155**, 1–61 (2004).
31. Strickland, B. K., Demarais, S. & Gerard, P. D. Variation in Mass and Lactation Among Cohorts of White-tailed Deer Odocoileus virginianus. *Wildl. Biol.* **14**, 263–271 (2008).
32. DeYoung, C. A. et al. *Density Dependence in Deer Populations: Relevance for Management in Variable Environments* (Hewitt Wildlife Science, 2007).
33. Folks, D. J. et al. Drought but not Population Density Influences Dietary Niche Breadth in White-tailed Deer in a Semiarid Environment. *Ecosphere* **5**, 1–15 (2014).
34. Fulbright, T. E. et al. Forb Standing Crop Response to Grazing and Precipitation. *Rangel. Ecol. Manag.* **79**, 175–185 (2021).
35. Kharouba, H. M. & Wolkovich, E. M. Lack of Evidence for the Match-Mismatch Hypothesis Across Terrestrial Trophic Interactions. *Ecol. Lett.* **26**, 955–964 (2023).
36. IPCC. *IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (Eds.)]*. https://www.ipcc.ch/report/ar6/syr/ https://doi.org/10.59327/IPCC/AR6-9789291691647 (IPCC, 2023).
37. Gaillard, J. M., Festa-Bianchet, M. & Yoccoz, N. G. Population Dynamics of Large Herbivores: Variable Recruitment with Constant Adult Survival. *Trends Ecol. Evol.* **13**, 58–63 (1998).
38. Hossain, M. L. & Beierkuhnlein, C. Enhanced Aboveground Biomass by Increased Precipitation in a Central European Grassland. *Ecol. Process.* **7**, 1–13 (2018).
39. La Pierre, K. J., Blumenthal, D. M., Brown, C. S., Klein, J. A. & Smith, M. D. Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient. *Ecosystems* **19**, 521–533 (2016).
40. Ginnett, T. F. & Young, E. B. Stochastic Recruitment in White-tailed Deer Along an Environmental Gradient. *J. Wildl. Manag.* **64**, 713–720 (2000).
41. Michel, E. S., Jenks, J. A., Kaskie, K. D., Klaver, R. W. & Jensen, W. F. Weather and Landscape Factors Affect White-tailed Deer Neonate Survival at Ecologically Important Life Stages in the Northern Great Plains. *PLoS One*. **13**, 0195247 (2018).
42. Garel, M. et al. Population Abundance and Early Spring Conditions Determine Variation in Body Mass of Juvenile Chamois. *J. Mammal.* **92**, 1112–1117 (2011).
43. Gaillard, J. M. et al. Early Survival in Roe Deer: Causes and Consequences of Cohort Variation in Two Contrasted Populations. *Oecologia* **112**, 502–513 (1997).
44. Andersen, R., Gaillard, J. M., Linnell, J. D. C. & Duncan, P. Factors Affecting Maternal Care in an Income Breeder, the European Roe Deer. *J. Anim. Ecol.* **69**, 672–682 (2000).
45. Michel, E. S., Demarais, S., Strickland, B. K., Belant, J. L. & Castle, L. E. Body Mass Influences Maternal Allocation More Than Parity Status for a Long-lived Cervid Mother. *J. Mammal.* **100**, 1459–1465 (2019).
46. Thorne, E. T., Dean, R. E. & Hepworth, W. G. Nutrition During Gestation in Relation to Successful Reproduction in Elk. *J. Wildl. Manag.* **40**, 330–335 (1976).
47. Aubin, G. R. et al. Survival of White-tailed Deer Fawns on Marine Corps Base Quantico. *J. Wildl. Manag.* **86**, 22180 (2022).
48. Heffelfinger, L. J. et al. Timing of Precipitation in an Arid Environment: Effects on Population Performance of a Large Herbivore. *Ecol. Evol.* **8**, 3354–3366 (2018).

49. Hediger, J. A. et al. Physiological Carry-over Effects of Variable Precipitation are Mediated by Reproductive Status in a Long-lived Ungulate. *Conserv. Physiol.* **12**, (2024).
50. Douhard, M. et al. Variation in Adult Body Mass of Roe Deer: Early Environmental Conditions Influence Early and Late Body Growth of Females. *Ecology* **94**, 1805–1814 (2013).
51. Michel, E. S. et al. Improved Nutrition Cues Switch from Efficiency to Luxury Phenotypes for a Long-lived Ungulate. *Ecol. Evol.* **6**, 7276–7285 (2016).
52. Monteith, K. L., Schmitz, L. E., Jenks, J. A., Delger, J. A. & Bowyer, R. T. Growth of Male White-Tailed Deer: Consequences of Maternal Effects. *J. Mammal.* **90**, 651–660 (2009).
53. Pettorelli, N. et al. Variations in Adult Body Mass in Roe Deer: The Effects of Population Density at Birth and of Habitat Quality. *Proc. R Soc. Lond. B Biol. Sci.* **269**, 747–753 (2002).
54. Solberg, E. J., Loison, A., Gaillard, J. M. & Heim, M. Lasting Effects of Conditions at Birth on Moose Body Mass. *Ecography* **27**, 677–687 (2004).
55. Hewison, A. M. et al. Reproductive Constraints, Not Environmental Conditions, Shape the Ontogeny of Sex-Specific Mass–Size Allometry in Roe Deer. *Oikos* **120**, 1217–1226 (2011).
56. Foley, A. M. et al. Fine-scale Phenotypic Variation of a Large Herbivore in a Pulsed Environment. *Ecosphere* **15**, e4921 (2024).
57. Plard, F. et al. The Influence of Birth Date via Body Mass on Individual Fitness in a Long-lived Mammal. *Ecology* **96**, 1516–1528 (2015).
58. Moen, A. N. *Wildlife Ecology: An Analytical Approach* (W.H. Freeman, 1973).
59. PRISM Group at Oregon State University. https://prism.oregonstate.edu/.
60. Crider, B. L. et al. Influence of White-tailed Deer Population Density on Vegetation Standing Crop in a Semiarid Environment. *J. Wildl. Manag.* **79**, 413–424 (2015).
61. DeYoung, C. A. et al. Linking White-Tailed Deer Density, Nutrition, and Vegetation in a Stochastic Environment. *Wildl. Monogr.* **202**, 1–63 (2019).
62. Gann, W. J. et al. Vegetation Response to White-tailed Deer Density and Enhanced Nutrition. *Wildl. Monogr.* **202**, 1–63 (2019).
63. Gann, K. R. et al. Deer Density Effects on White-tailed Deer Diets and Foraging Behavior Under Natural Nutrition. In *Linking White-tailed Deer Density, Nutrition, and Vegetation in a Stochastic Environment* **202** 19–26 (2019).
64. Cook, R. S., White, M., Trainer, D. O. & Glazener, W. C. Mortality of Young White-Tailed Deer Fawns in South Texas. *J. Wildl. Manag.* **35**, 47–56 (1971).
65. Krausman, P. R., Hervert, J. J. & Ordway, L. L. Capturing Deer and Mountain Sheep with a Net-Gun. *Wildl. Soc. Bull.* **13**, 71–73 (1985).
66. Foley, A. M. et al. Accuracies and Biases of Ageing White-tailed Deer in Semiarid Environments. *Wildl. Res.* **49**, 237–249 (2021).
67. Hirth, D. H. Mother-Young Behavior in White-tailed Deer, Odocoileus virginianus. *Southwest. Nat.* **30**, 297–302 (1985).
68. Therrien, J. F., Côté, S. D., Festa-Bianchet, M. & Ouellet, J. P. Maternal Care in White-tailed Deer: Trade-off Between Maintenance and Reproduction Under Food Restriction. *Anim. Behav.* **75**, 235–243 (2008).
69. Verme, L. J. Reproductive Patterns of White-tailed Deer Related to Nutritional Plane. *J. Wildl. Manag.* **33**, 881–887 (1969).
70. TPWD. The Rut in White-tailed Deer. https://tpwd.texas.gov/huntwild/hunt/planning/rut_whitetailed_deer/.
71. Ortega-S, J. A., Lukefahr, S. D. & Bryant, F. C. Optimum Stocking Rate, Monitoring, and Flexibility: Key Components of Successful Grazing Management Programs. *Rangelands* **35**, 22–27 (2013).
72. Akaike, H. Maximum Likelihood Identification of Gaussian Autoregressive Moving Average Models. *Biometrika* **60**, 255–265 (1973).
73. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, 2002).
74. Bolker, B. M. et al. Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).
75. Bates, D. M. *lme4: Mixed-effects Modeling with R*. (2010).

Acknowledgements

We thank the East Foundation and the Patton Center for Deer Research for their funding and support during this research. Additional support was provided by the Hixon Fellowship, the Barrientos Scholarship, and the Houston Safari Club Dan L. Duncan Scholarship. J. A. Ortega-Sanchez, K. Gann, M. Rice, and S. Rankins coordinated capture activities during 2011–2020, assisted by numerous student volunteers from Texas A&M University-Kingsville, Southwest Texas Junior College, Stephen F. Austin State University, Sul Ross State University, Tarleton State University, Texas A&M University, Texas State University, and Texas Tech University. A. Montalvo, A. Woodard, J. Haynes, A. Lopez, R. Douglas, S. Vasquez, and M. Robinson of the East Foundation were instrumental in field logistics and activities. A. Tanner and H. Abernathy reviewed earlier drafts of the paper. All clipart was obtained from the University of Maryland Center for Environmental Science Integration and Application Network. B. Green assisted in editing conceptual figures. This is #25-114 of the Caesar Kleberg Wildlife Research Institute and #096 of the East Foundation.

Author contributions

M.L.H. and M.J.C. conceived the ideas of this manuscript. All authors collected the data. M.L.H. developed the analytical framework and analyzed the data. M.L.H. developed and designed all figures (with illustrations provided by the University of Maryland Center for Environmental Science Integration and Application Network and Breanna Green). M.L.H. led the writing of the original manuscript. All authors contributed critically to all drafts and gave final approval for publication.

Funding

The authors gratefully acknowledge the financial support provided by the East Foundation and the Patton Center for Deer Research.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-026-40861-4.

Correspondence and requests for materials should be addressed to M.L.H.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

© The Author(s) 2026