PHYSIOLOGICAL ECOLOGY – ORIGINAL RESEARCH

Milk composition in a wild mammal: a physiological signature of phenological changes

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Abstract

Understanding how spring phenology influences early life can provide important insights into drivers of future development and survival. We combined unique, long-term data from a bighorn sheep population and satellite-derived phenology indices to quantify the relative importance of maternal and environmental influences on milk composition and lamb overwinter survival. Based on 216 milk samples from 34 females monitored over 6 years, we found that longer snow-free and vegetation growing seasons increased milk fatty acid, iron and lactose concentrations. Structural equation modelling revealed no causality between milk energy content, lamb weaning mass and lamb overwinter survival. Our results suggest that spring conditions can affect milk energy content, but we did not detect any effect on lamb overwinter survival either directly or indirectly through lamb weaning mass. The effect of green-up date on milk composition and energy content suggests that herbivores living in seasonal environments, such as the bighorn sheep, might rely on a strategy intermediate between 'capital' and 'income' breeding when energy demands are high.

Keywords Climate change · Lactation · Maternal effects · Timing of parturition · Vegetation phenology

Introduction

Early-life conditions can have crucial fitness consequences (Lindström 1999). Parental care is assumed to benefit offspring ontogeny, with effects sometimes lasting through

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adulthood (Lindström 1999). Ability to provide parental care, however, may vary according to environmental conditions. For long-lived herbivores in temperate environments, shifts in spring phenology—the timing of key biological events—induced by climate change (Parmesan 2006) can prolong the snow-free period, potentially allowing individuals to obtain more resources and provide greater parental care (Ozgul et al. 2010). As a consequence, we could expect higher survival and increased population size (Ozgul et al. 2010). In contrast, failure to synchronize reproductive phenology, starting with timing of parturition, to changes in peak forage availability may have detrimental consequences at the population level, through long-lasting effects on female adult mass and reduced juvenile survival (Plard et al. 2014). The timing of key reproductive events in wild animal populations is assumed to have evolved to synchronize with seasonal resource availability at lower trophic levels (Both et al. 2009), but we still know little about the relationships between environmental cues and optimal timing, or how this relationship will be affected by environmental changes (McNamara et al. 2011).

Phenological changes are frequently documented in wild organisms in response to climate change (Parmesan 2006). In birds, the timing of egg laying often varies with

temperature (Crick et al. 1997; Charmantier et al. 2008). Most studies, however, have been conducted on passerine birds which rely on income breeding to meet the energetic costs of reproduction (Meijer and Drent 1999; Thomas et al. 2001). In those species, nestling feeding is dependent on daily food availability; thus optimal timing of breeding is a critical determinant of future reproductive success and, ultimately, fitness (Thomas et al. 2001). At the other end of the life-history gradient, capital breeders depend mostly on stored body resources (Fletcher et al. 2013) to 'finance' reproduction. Placental mammals such as ruminants increase energy expenditure during lactation up to four times their basal metabolic rate (Oftedal 1985). To support the high energetic costs of lactation, fitness is assumed to be maximized when timing of parturition 'matches' vegetation growth (Oftedal 1985). While some studies have investigated the effect of spring phenology on birth timing (Thomas et al. 2001; Visser et al. 2012), few have evaluated how spring phenology can influence physiological aspects of maternal care in long-lived species. Both maternal reserves and vegetation phenology may affect timing of breeding or traits linked to maternal care such as food provisioning to offspring. For example, in domestic sheep variation in milk components early in lactation reflects the amount of maternal reserves (Wohlt et al. 1981). A species' position along the capital-income breeding gradient may determine how its life-history traits such as timing of breeding will respond to changes in the phenology of its main food resources (Jönsson 1997).

Here, we focus on the relationships between milk nutrients and their associations with timing of parturition, vegetation phenology and offspring traits in a natural population of ungulates to test the hypothesis that milk composition and juvenile overwinter survival are affected by spring phenology. Milk plays a crucial role in offspring development (Hinde and Milligan 2011). In the first hours of life, immunoglobulins in colostrum boost the newborn immune system (Hurley and Theil 2011). Milk also contains important nutrients such as minerals that, together with immunoglobulins, enzymes and hormones, enhance offspring immunity, growth and development (Hamosh 2001; Gallego et al. 2009). Studies in primates (Hinde et al. 2009), marine (Lang et al. 2009) and domestic mammals (Gallego et al. 2009) have established that milk production and composition are important for juvenile growth, weaning mass and survival which in turn increase population growth rate by affecting recruitment (Ozgul et al. 2010). Fewer studies, however, have asked how change in spring phenology affect milk composition and whether milk characteristics correlate with offspring growth and survival in terrestrial wild eutherians (see Cork 1991; Quesnel et al. 2017 for examples on marsupials). Thus, much of our current knowledge is based on short-term studies (Skibiel and Hood 2015; Quesnel

et al. 2017) focusing mainly on fatty acid and milk protein content. In bighorn sheep (*Ovis canadensis*), milk composition varies from year to year (Renaud et al. 2019), but it is unknown whether plant phenology and maternal body condition explain inter-individual and inter-annual differences in milk composition, including minerals.

In this study, we were interested in how the relative importance of maternal reserves and vegetation quality for milk composition changes from birth and through the course of lactation. We specifically aim to (1) investigate how spring phenology drives variation in milk composition; and (2) assess how milk composition influences weaning mass and overwinter survival, two important fitness-related traits in our model species (Pelletier et al. 2007; Douhard et al. 2018). Milk composition is strongly affected by inter-annual environmental variations and, to a lesser extent, by individual differences among mothers (Renaud et al. 2019). Building on those findings, we hypothesize that inter-annual variations in milk composition can be affected by spring phenology. We further hypothesized that major milk macronutrients—fatty acids, proteins and glucose—indirectly affect lamb overwinter survival through effects on weaning mass. We used detailed individual data to answer fundamental questions on how spring phenology influences life history in a wild vertebrate.

Methods

Field and laboratory techniques

The Ram Mountain bighorn sheep population in Alberta, Canada (52° N, 115° W, elevation 1080–2170 m) has been monitored since 1971. Sheep are captured in a corral trap baited with salt and observed daily from late May to late September. Most lambs are marked during their first summer and their sex is recorded along with maternal identity (Jorgenson et al. 1993). Weaning occurs in mid-September; later suckles are rare and very short (Festa-Bianchet 1988). Parturition date was estimated from 1992 to 2017 (except for 1993) based on morphology, including lamb size, presence of the umbilical cord and dark grey coat (Geist 1971). Because ewes isolate themselves for 2–3 days post-partum before they join other ewes (Festa-Bianchet 1988), the number of days since a ewe was last seen before giving birth helped us estimate lamb birthdate.

Most adult ewes are captured and weighed 2–5 times during each field season. We adjusted individual female mass to June 5 and September 15, and individual lamb mass to June 15 and September 15 (Martin and Pelletier 2011). From 2011 to 2016, we collected milk samples (5–15 mL) from ewes at each capture and stored them at − 20 °C until laboratory analyses. We quantified milk composition for 216

samples from 34 mothers of 76 lambs (1.06 ± 1.64 SD samples/mother/year or 2.84 ± 1.45 SD samples/lamb). We could not quantify milk yield nor time since last suckling. We estimated milk fatty acid, protein, glucose and lactose concentrations as described in Renaud et al. (2019). We quantified macronutrients using colorimetry while minerals—calcium (Ca), iron (Fe), magnesium (Mg), phosphorus (P), potassium (K), sodium (Na) and zinc (Zn)—were analysed by inductively coupled plasma-optical emission spectroscopy (ICP; Perkin-Elmer ICP Optima 4300DV). Fatty acid, protein, glucose and lactose concentrations are expressed as a function of milk volume ($mg\ mL^{-1}$) while mineral concentrations are reported in parts per million (ppm). To investigate if milk energy content affected lamb weaning mass and overwinter survival, we calculated the energy derived from fatty acids, protein and glucose concentrations per unit volume. We assumed that energy values were 24.6 kJ g^{-1} for protein, 38.1 kJ g^{-1} for lipid and 16.1 kJ g^{-1} for glucose (Oftedal et al. 2014).

Extraction of phenology indices

We used data acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) (Justice et al. 1998) to quantify plant phenology throughout the sampling region in autumn and spring seasons (Table S1). We extracted Julian dates (1 Jan = 1 JD) of the maximal increase and decrease in time series of seven different vegetation indices (Table S1). We refer to these as 'green-up' and 'green-down' dates for spring and autumn phenologies, respectively. 'Green-down' dates correspond to vegetation senescence and signal the end of the growing season: the number of days between green-up and green-down, hereafter referred to as 'Season length'. For snow, dates represent the maximal rate of change in the probability of snow on the ground. We refer to spring dates as 'Snowmelt date' and to autumn dates as 'Snowfall date'. The season length based on snow cover was the difference, in Julian days, between 'Snowfall date' and 'Snowmelt date', hereafter referred to as 'Snow-free' season.

After examining the correlations among raw phenology indices (Table S2), we included in our analyses two variables that best described spring phenology: green-up date, corresponding to the maximal increase in gross primary productivity (GPP) and snowmelt date, corresponding to the maximal rate of change in the probability of snow on the ground (see Supplementary Information for details).

Multivariate hierarchical modelling of milk composition

Our next analysis decomposed the multiple sources of variation in milk composition using a multivariate framework suitable for the analysis of ecophysiological data (Renaud

et al. 2019). This analysis used individual-level observations to include all repeated female observations within and over years. We used Bayesian Multivariate Hierarchical Modelling (MHM, Warton et al. 2015, Ovaskainen et al. 2017) to investigate the joint responses of milk components to maternal traits, lamb traits and spring phenology. We tested the effects of spring phenology dates and season lengths in two separate models. To ensure that the milk sampling period matched that of phenology dates, we included in this analysis only milk samples collected before June 19, the latest green-up recorded (mean sample/female $\pm$ SD = 1.46 ± 0.59). To enhance detection of phenology effects on milk composition, we selected a subset of nutrients for which inter-annual variance was $\geq 30\%$ of the total explained variance, equivalent to the average variation explained across all nutrients in an earlier analysis of milk composition (see Renaud et al. 2019 for more details). Based on correlations in this reduced dataset, we kept maternal June mass (correlation with September mass: $r = 0.80$, $P < 0.001$) and snowmelt date (correlation with GPP date: $r = 0.98$, $P < 0.001$) in our final analyses.

We modeled this subset of milk components by assuming a Gaussian error (Renaud et al. 2019). In addition to snowmelt date and snow-free season, we accounted for sampling year as a random effect since we were interested in inter-annual variations in milk composition. We also included maternal identity and milk sample number as random effects to respectively model inter-individual and residual (within-individual) variances. Sample number accounted for variation in milk composition that could not be modeled using any of the other variables considered, including female identity or sampling year; it thus represents the variation that a female expresses over repeated milk measurements within seasons or over years. Maternal traits included summer mass gain and winter mass loss (controlling for June mass and previous September mass, respectively, because changes depend on initial mass (Pelletier et al. 2007)). We included age (days since estimated birth), sex and birth date as lamb traits; sex was dropped from the model because it showed no effect on milk composition.

Iron concentration was log-transformed to meet normality requirements. All other response variables were normally distributed. Prior to analyses, we centered and scaled all continuous variables to remove the effect of measurement units. The model parameters were estimated using Markov chain Monte Carlo (260,000 iterations including 60,000 burn-in iterations and a thinning of 200, for a total of 1000 remaining iterations for estimation and inference). We assessed model convergence using the Gelman–Rubin statistics (Gelman and Rubin 1992). To do so, we carried 5 runs, each with a different set of starting values. All values of the Gelman–Rubin statistics were below 1.01 and the multivariate statistic was 1.01. Parameters are assumed to have converged

when the Gelman–Rubin statistic is below 1.1. We quantified the explanatory power of models with a coefficients of determination (R^2), calculated for each response variable and for the multivariate response, which is calculated as the average R^2 over all independent milk components. Weakly informative prior specifications were as proposed by Bhattacharya and Dunson (2011) for latent variables and by Ovaskainen et al. (2017) for fixed explanatory variables. We present parameter estimates with 95% credibility intervals (i.e. slope [LCI, UCI]). All analyses presented in this section were carried out with the 'HMSC' package (Blanchet et al. 2017) used through the R statistical language version 3.5.1 (R Core Team 2018).

Path analysis of lamb weaning mass and overwinter survival

Lamb age (in days) and sampling year influence milk composition (Renaud et al. 2019). We adjusted each milk component by including both lamb age (continuous) and year (factor) as fixed variables in a linear mixed-effects model for each milk component. We included a random effect of lamb age over mother identity in all models, i.e., an individual-by-lamb age interaction to account for individual females adjusting milk composition differently with lamb age. We were interested in how mothers allocated energy to very young lambs that survived the neonatal stage. Using the beta-coefficients of these mixed regressions, each milk component was thus adjusted to a lamb age of 10 days to approximate milk composition during early lactation. We then calculated the energy derived from adjusted milk macronutrients in kJ g^{-1} per unit volume (mL) (Oftedal et al. 2014).

To disentangle the direct and indirect effects of energy derived from adjusted milk components on lamb weaning mass and overwinter survival over 6 years, we analysed the datasets on adjusted milk energy content, phenology, lamb weaning mass, and overwinter survival (0 = died or 1 = survived) using Piecewise Structural Equation Modelling (SEM, number of observations (n) = 65) (Lefcheck 2016). Piecewise SEMs are conceptually similar to classical path analysis but solve each component model separately. Thus, piecewise SEM allows for models with their own sampling distributions and small sample sizes (Lefcheck 2016).

We first fit the three component models (response variables: milk energy content, lamb weaning mass and overwinter survival) as generalized linear-mixed effect models (GLMMs) with their appropriate error distributions (Gaussian for all but overwinter survival which is binomial). All three models tested for an effect of parturition date on milk composition and lamb weaning mass (Fig. S1). The relationship between weaning mass and parturition date varies by lamb sex, and among late-born lamb males have lower

survival than females (Feder et al. 2008). The relationships between parturition and milk energy and between lamb sex and milk energy tested whether, independently of green-up date, parturition date and lamb sex influenced milk energy content. The effect of parturition date on lamb weaning mass tested whether, given equal energy content (per mL), late-born lambs would be lighter in September. Given equal energy content, we expected male lambs to be heavier than female lambs. We hypothesized that the timing of spring green-up would influence adjusted milk composition, lamb weaning mass and maternal variables. A late green-up would leave less time for lambs and their mothers to benefit from high-quality forage, resulting in lower weaning mass and energy allocation to lactation. We expected that late green-up would reduce milk energy, independently of parturition date, by forcing females to use body stores for early lactation. To test the amount of energy a female allocated to lactation, we included summer mass gain controlling for initial mass in June, hereafter referred to as residual mass gain. We included maternal June mass—a proxy of initial capital store—and residual summer mass gain—a proxy of allocation to lactation, or milk volume (Lang et al. 2011)—as two independent variables in all models. Mass gain is influenced by several environmental variables other than milk production (Douhard et al. 2018). By including mass gain and June mass in our model, we assumed these variables were correlated to milk volume, not substituting it. We modeled maternal mass in June as a function of green-up date, and we initially expected that timing of green-up would allow lactating females to compensate for the energetic costs of lactation (Hamel and Côté 2009). Increased foraging could thus buffer the effect of milk production on summer mass gain, thus buffering variation in summer mass gain. We could only test an effect of residual mass gain on milk composition, but this effect was not statistically significant and thus was removed from further analyses. Finally, we tested the effect of predation on lamb overwinter survival and on maternal variables. Predation is either weak or strong depending on the presence of sheep-specialist cougars (Festa-Bianchet et al. 2006), which was the case only in 2013. Each component model had maternal identity and sampling year (thirty and six levels, respectively) as random effects to account for non-independence of observations within years and mothers.

We compared five SEMs to determine the key direct and/or indirect effects of milk energy and maternal mass gain on lamb overwinter survival (Fig. S1). Our first path model, or 'null' model (Figs. S1a, 3a), tested the prediction that lamb overwinter survival was independent of any variable included in the causal model. Our second path model (Fig. S1b), tested the prediction that milk composition, maternal June mass and summer mass gain, indirectly affect lamb survival by increasing lamb weaning mass. Our third path model (Fig. S1c) tested whether milk composition, not mass

gain, directly affected survival through mechanisms other than lamb weaning mass, for example by increasing immunity, bone and motor development and other physiological systems. These models assumed that summer mass gain and June mass only directly affect lamb weaning mass. Two additional models tested whether summer mass gain and June mass influence lamb survival independently of lamb weaning mass (Fig. S1d and e).

We used d-separation (Shipley 2016) to test whether each SEM fit was improved by the inclusion of identified missing paths. The d-separation test generates a Fisher's C test statistic, which can be used to assess overall fit of the SEM and to calculate an Akaike's information criterion corrected for small sample sizes (AICc) used for model selection (Shipley 2016). As we were mostly interested in the direct or indirect effect of milk, either composition or maternal mass gain, on survival, we compared the five candidate models and selected the SEM with the lowest AICc value. Models including an effect of green-up date or predation on residual mass gain were all rejected. Predation was not statistically significant and was thus removed from final models. For the best-fit SEM, we extracted all coefficients to determine the strength of paths. We conducted all statistical analyses in R version 3.5.1 (R Core Team 2018). We used the R package 'piecewiseSEM' (Lefcheck 2016) for d-separation tests and report parameter estimates and associated 95% confidence intervals (i.e. slope [LCI, UCI]) as given by the path models coefficients.

Results

Temporal trends in phenology indices

From 2001 to 2016, mean date of green-up was May 27 ± 15.88 SD (median: May 31, Fig. 1) and mean snowmelt was April 30 ± 14.77 SD (median: May 4). Growing season length averaged 102.41 days ± 20.78 SD based on GPP and snow-free season, 166.06 days ± 18.81 SD. There was no detectable trend in green-up ($- 0.99$ [$- 2.63$, 0.65]) or snowmelt dates over years ($- 0.78$ [$- 2.19$, 0.63]); a quadratic effect of year gave similar results.

Causes of variation in milk composition using MHM

On average, the model including snowmelt dates explained 77.0% of variation in milk composition (range of R^2 across milk components $= 0.66$–0.86) but effect of snowmelt date was not different from zero across milk markers (Fig. S2a). In the model testing length of snow-free season, global R^2 was 0.64 (range 0.57−0.68). The strongest effect of snowmelt date was on milk fatty acid concentration ($- 0.81$

Fig. 1 Density distribution of green-up (on the right; in green in the online version) and snowmelt dates (on the left; in orange in the online version) as extracted from phenology time series, Ram Mountain, Alberta, Canada, 2000–2017. Julian day 150 is equivalent to May 30 in non-leap years
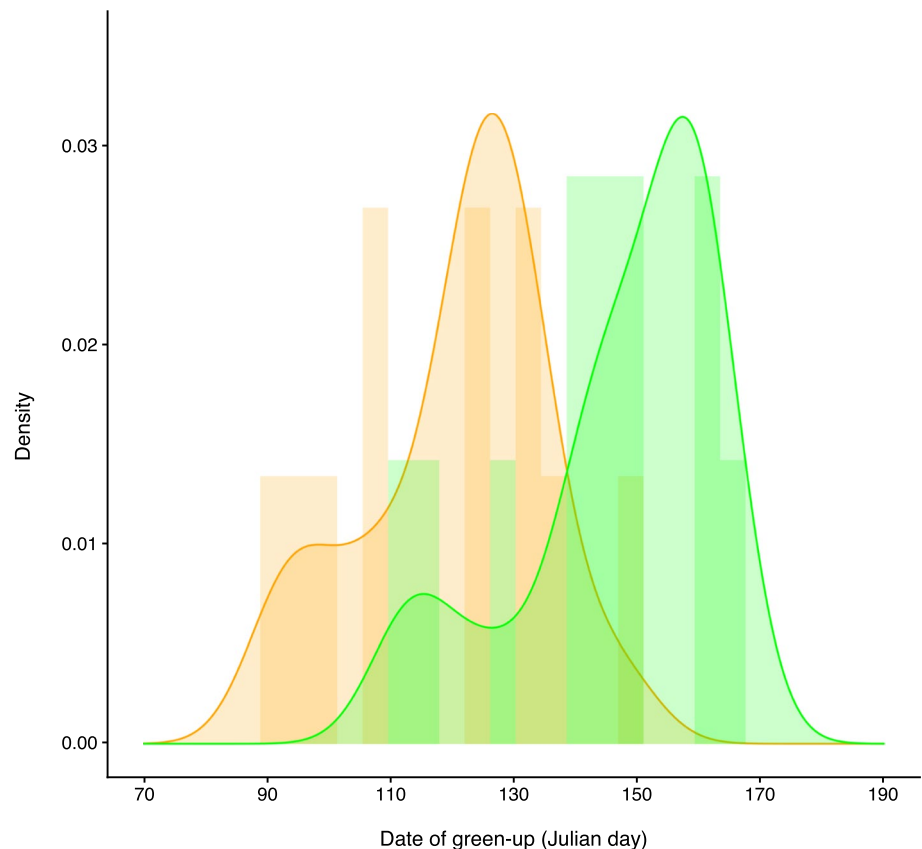
[− 1.27, − 0.25, Fig. 2a). Snowmelt date also affected iron concentration (− 0.69 [− 1.26, − 0.09). Sampling year R^2 was most variable across milk components, ranging from 0.12 to 0.52. R^2 for female identity ranged from 0.07 to 0.20. R^2 ranged from 0.04 to 0.36 for snowmelt date across milk components. In the model testing season length, year was most variable across milk components (average R^2_{year} = 0.30, average $R^2_{female\ identity}$ = 0.05). Length of snow-free season explained up to 30% of variation in milk composition (range of R^2 0.04–0.30). Season length affected fatty acids (0.63 [0.35, 0.89], Fig. 2b). Later parturition was associated with lower Na concentrations (− 0.16 [− 0.28, − 0.04]) and higher fatty acid concentrations (0.16 [0.05, 0.26], Fig. 2b) in this model. Maternal June mass affected milk fatty concentration composition (0.12 [0.01, 0.23]).

## SEMs of lamb weaning mass and overwinter survival

None of the SEM were rejected by d-separation, suggesting that the data supported the implied independences for these five causal models (Shipley 2016). We used AICc to compare simplified models. Simplified models excluded direct paths between green-up date and lamb weaning mass, and paths between predation and lamb or maternal variables. The

'null' model had an AICc of 76.83 (Figs. S1a, 3a). Other models had AICc values of, respectively, 79.92 (Fig. S1b), 75.52 (Fig. S1c), 73.24 (Fig. S1d) and 84.45 (Fig. S1e). Only one model (Figs. S1d, 3b) thus had an AICc notably lower than the 'null' model; this model explained 13% of variation in lamb overwinter survival. Male lambs had lower overwinter survival than females. Maternal mass gain and milk energy content did not influence lamb overwinter survival (Fig. 3b). Lamb weaning mass was influenced by the direct effects of parturition date (− 0.67 [− 0.82, − 0.51]), lamb sex (0.20 [0.10, 0.74], and maternal June mass (0.28 [0.09, 0.46]). Males were heavier than females at weaning, independently of parturition date. Both late green-up (− 0.94 [− 1.16, − 0.72]) and early parturition (0.09 [0.04, 0.14]) were associated with low milk energy content (Fig. 3a, b).

Discussion

Phenological changes in reproductive traits following climate change are well documented (Parmesan 2006) but most evidence in vertebrates comes from birds (Charmantier et al. 2008; Visser 2008; Both et al. 2009; Visser et al. 2012), especially small passerines (Meijer and Drent 1999). We

Fig. 2 Relationship between maternal covariates and spring phenology for fatty acid concentrations in bighorn sheep, Ram Mountain, Alberta, Canada, 2011–2016 (*n* = 220). (**a**) Snowmelt date and (**b**) length of snow-free season (referred to as snow-free length) was tested as an explanatory variable in the multivariate model. Estimates are effect sizes of fixed effects for fatty acid concentration. Sampling year, mother's identity and a sample-level factor were included as random effects. The horizontal line represents the 95% credibility intervals and the grey dot, the mean. The vertical grey line is drawn on zero for reference
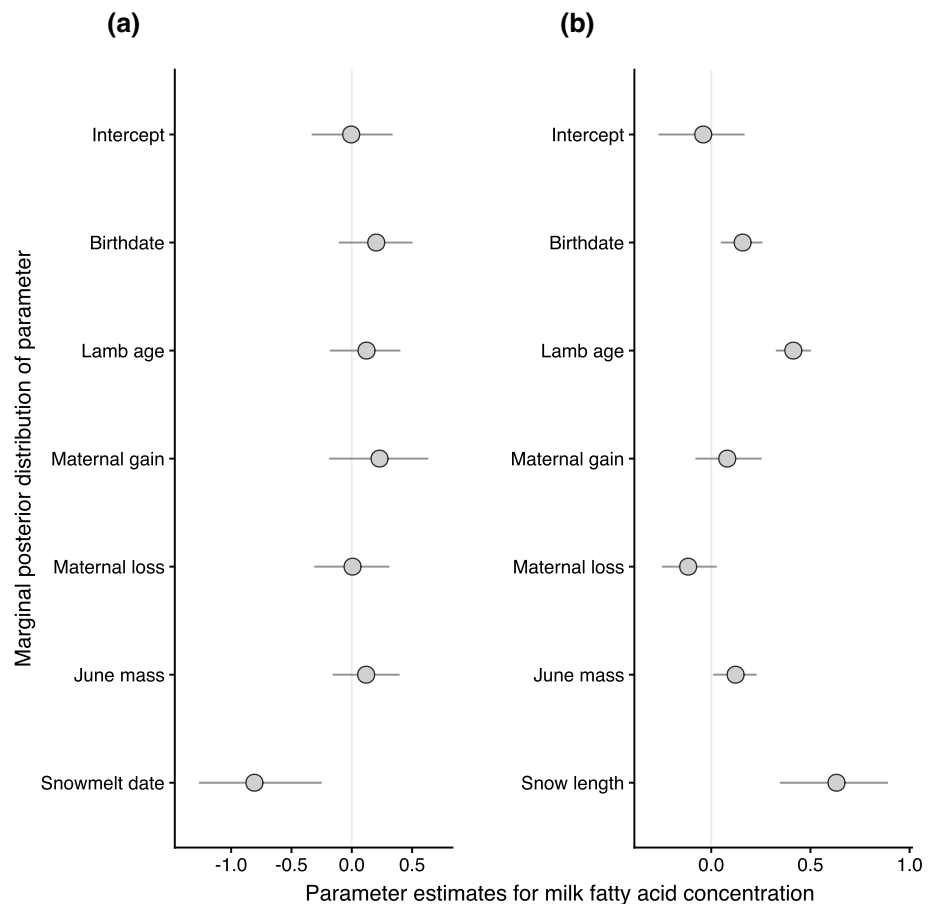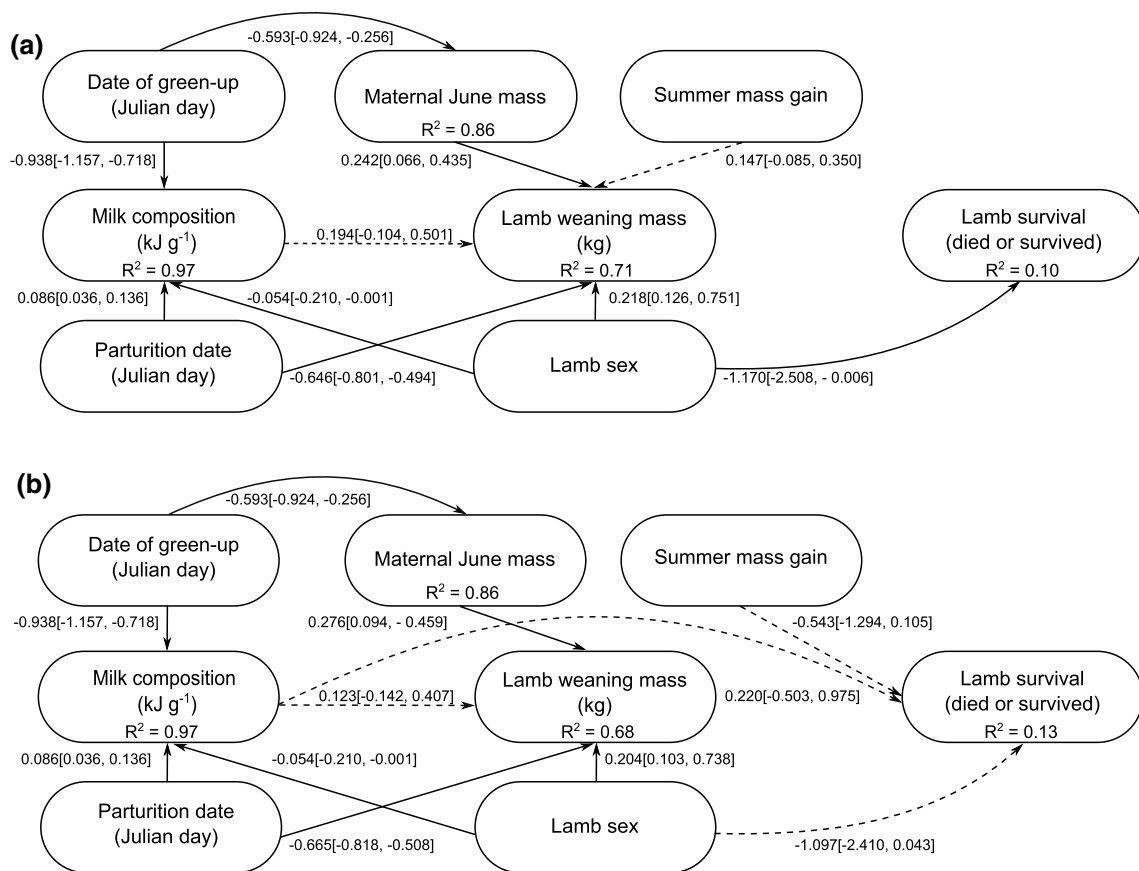
Fig. 3 Final path diagrams of causal effects between phenology, variation in milk composition, and bighorn lamb mass and survival at Ram Mountain, Alberta, Canada, 2011–2016 ($n = 65$). We first tested (**a**) the absence of effects on survival and (**b**) a direct effect of milk energy and maternal summer mass gain on lamb survival. Arrows indicate paths included in the models. Solid lines indicate statistically significant effects of a variable on another. Dashed arrows indicate not statistically significant paths included in a model. Standardized path coefficients and 95% confidence intervals are indicated directly on corresponding paths

quantified temporal variation in spring phenology and investigated how it influenced phenotypic traits during the first year of life, given that early-life traits can have long-term fitness effects (Lindström 1999). Longer plant growing seasons increased milk fatty acid concentrations, but we found no causal relationships between milk energy content, lamb weaning mass and lamb overwinter survival. Our results suggest that spring vegetation phenology influences bighorn sheep milk composition, but we detected no effect of phenology on milk energy content and lamb overwinter survival, either directly or indirectly through effects on lamb weaning mass. Large mammals in seasonal environments are thought to rely partly on forage resources to sustain the energetic costs of lactation (Fletcher et al. 2013).

We found that late spring green-up is associated with low milk energy content. However, milk energy content does not influence lamb weaning mass and overwinter survival, contrasting with results for other mammals (Lang et al. 2009; Skibiel and Hood 2015). Milk quantity, rather than milk composition, likely drives lamb summer

growth but we did not measure that variable in the wild. Our proxy of milk volume, maternal mass change during summer was, however, not associated with lamb weaning mass. Although it is often difficult to collect both milk composition and volume on wild mammals, relative contribution of milk to solid food in the diets of weanlings of primates have been compared using stable isotope analyses (Bădescu et al. 2017). Lambs forage during summer thus do not entirely depend on maternal milk for growth, unlike in some other mammal species such as marmots (Ozgul et al. 2010). Interestingly, only maternal mass loss influenced milk fatty acid concentration, suggesting that resource intake through foraging may be more important than endogenous reserves for lactation in this species. This finding is surprising given that body mass increases reproductive success in bighorn sheep females (Festa-Bianchet 1998). Our analyses, however, were limited to females whose lambs survived long enough for their mothers to produce milk samples and excluded individuals that died at a young age (Grafen 1988), thus limiting variability

in milk energy content or female body condition in our sample. Finally, we could not determine the exact date of weaning of individual lambs and consequently we may have missed some variation in weaning mass, limiting our ability to detect possible weak correlations between milk composition, weaning mass and survival with our 6 years of data on milk composition.

Long 'snow-free' seasons increased milk fatty acid and iron concentrations, suggesting that abundant forage directly facilitates allocation of resources to lactation perhaps through increased fat gain, but we did not detect any effect of mother summer mass gain on fatty acid concentration. Studies of wild mammals usually do not measure milk composition, limiting our ability to test the links between change in spring phenology and milk composition. Indeed, studies commonly use indirect proxies of energy allocation to food provisioning, such as mass changes or variation in percent of body fat, to assess if variation in these proxies result from variation in vegetation phenology. However, food is more than energy, and a detailed understanding of relative nutrient intake can be crucial to understand the fitness impacts of nutrition (Raubenheimer and Simpson 1999). Matching peak food abundance is often used as the driver of changes in energy allocation or body mass. In the Greater Yellowstone Ecosystem, migratory elk (*Cervus canadensis*) can track the green-up period and use habitat patches at peak forage quality for a longer period than resident elk. This behaviour can account for up to ~3.5% of variation in autumn body-fat levels, which is strongly associated with reproductive success in this species (Middleton et al. 2018). Similarly, following warmer spring air temperatures, yellow-bellied marmots (*Marmota flaviventris*) emerge earlier from hibernation and benefit from longer growing seasons, allowing greater mass gain in young and adults and increased population growth (Ozgul et al. 2010). Possibly, milk quality or quantity, as maternal summer nutrition was likely improved by longer plant availability, contributed to the observed mass gain in young marmots. Our study provided rare evidence and a direct assessment that vegetation phenology is associated with an important aspect of maternal care, milk composition.

We used unique, individual-based data to investigate the effects of vegetation phenology at the individual and physiological levels in a wild mammal. Our results suggest that bighorn ewes do not entirely sustain the costs of early lactation from stored energy reserves, and like several other large mammals rely on a strategy intermediate between 'capital' and 'income' breeding when energy demands are high. Young mammals could respond positively to phenological shifts with an increased mass gain during longer summers (Ozgul et al. 2010) but long-term effects of warmer or earlier springs on vegetation growth and herbivores are unknown (Buermann et al. 2018). If species cannot adjust to changes in ecosystem productivity

under climate change, the demographic consequences will threaten the persistence of wild populations.

Author contribution statement LAR, FGB, AAC and FP conceived the ideas and designed methodology. FP and MFB. run the long-term project. LAR and FR extracted all phenology indices. LAR and FR analysed the data. LAR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility The datasets analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Animals were captured and handled in compliance with the Canadian Council on Animal Care, under the approval of the Université de Sherbrooke Animal Care Committee (protocol number FP-2016-01 and MFB-2018-01—Université de Sherbrooke).

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