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Research

Berry production drives bottom–up effects on body mass and reproductive success in an omnivore

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Obligate herbivores dominate studies of the effects of climate change on mammals, however there is limited empirical evidence for how changes in the abundance or quality of plant food affect mammalian omnivores. Omnivores can exploit a range of different food resources over the course of a year, but they often rely on seasonally restricted highly nutritious fruiting bodies during critical life stages. Brown bears *Ursus arctos* in Sweden are dependent on berries for fattening before entering hibernation. We used a ten-year time series to evaluate the effect of temperature and snow on annual variation in berry abundance and how this variation affected bears. We found marked interannual variation in berry production of bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea*, that we could attribute in part to temperature during plant dormancy and flowering and precipitation during fruit ripening. Both, autumn weights of female bears and spring weights of yearling bears increased linearly with bilberry abundance. When bilberry abundance was low, lightweight female bears had a lower reproductive success than females in better condition. This effect vanished when food abundance was above average, indicating that lightweight females could compensate for their initial weight during good bilberry years. Our study highlights the importance of considering individuals' dynamic responses to variation in food availability, which leave some more vulnerable to food shortage than others. Individual life-history heterogeneity in response to resource variation likely affects long-term population recruitment. Our findings emphasize that Scandinavian bears can be dependent on a single food resource during a critical period of the year and are therefore less resilient to environmental change than expected for an omnivore. Future climate scenarios predict ambiguous trends for weather covariates that affected crucial stages of berry phenology, preventing a clear prognosis of how climate change may affect long-term bilberry production.

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Introduction

Climate change causes increased temperatures and precipitation at northern latitudes, in particular during the winter months (Christensen et al. 2007). A shorter duration of snow cover and an earlier onset of spring are already evident in northern areas, which markedly influences the production and phenology of plants and, in turn, the life history and population dynamics of herbivores (Post and Stenseth 1999, ACIA 2005). During the last decades, several long-term projects have documented how climate directly and indirectly affects many aspects of mammalian life histories via their food resources. Most of these studies focused on ruminants as model species (Mysterud et al. 2001, Pettorelli et al. 2007, Tveraa et al. 2013). However, the mechanisms determining how climate may affect populations and their food bases likely differ across taxonomic groups, depending on life history and diet. An understanding of the differences in these mechanisms is important for predicting future responses of different taxonomic groups, and in turn the resilience of the ecosystem, to climate change (Krebs and Berteaux 2006).

Omnivores have a simple digestive system and often rely on easily digestible and highly nutritious fruiting bodies, like berries or nuts, during limited time periods (Smith and Follmer 1972, Bojarska and Selva 2012). Next to changes in plant productivity (Post and Stenseth 1999) and a longer growing season (Inouye 2008), plant responses to a warming climate also include a shift in the timing of fruit ripening (Menzel et al. 2006, Gallinat et al. 2015) and altered fruit production (Chapman et al. 2005, Bokhorst et al. 2011). In this study, we address how omnivorous mammals are affected by annual variation in fruit production. We use the brown bear *Ursus arctos*, a large-bodied hibernating omnivore, as model species. In many populations, brown bears forage mainly on berries during the summer and autumn hyperphagia period, and berries are a key resource for building fat reserves necessary for hibernation (Bojarska and Selva 2012).

The few studies evaluating the indirect effects of climate change on small omnivorous hibernators found a crucial dependence between weight acquisition during hyperphagia and the timing of den entrance and emergence for reproductive success and winter survival (Inouye et al. 2000, Ozgul et al. 2010, Tafani et al. 2013). It is unclear whether similar constraints apply to larger hibernators, such as Ursids. Bears are extreme examples of capital breeders, in which resources accumulated prior to reproduction are used to meet energetic demands of reproduction and offspring rearing (Stearns 1992, Hilderbrand et al. 2000, Robbins et al. 2012, McLellan 2015). Bears mate in late spring/early summer (Steyaert et al. 2012) but implantation does not occur until females enter the winter den (Friebe et al. 2001). They are the only group that give birth during hibernation, sustaining themselves and their newborn cubs solely from body reserves acquired in the preceding autumn (Friebe et al. 2001). Lactation is energetically demanding and body condition during denning limits a females' reproductive ability (López-Alfaro et al. 2013). In large herbivores, reduced lifetime reproductive success has been documented for cohorts born in years with food shortage (Albon et al. 1987, Gaillard et al. 2000, Couturier et al. 2009). Bears may be more resilient to cohort effects on lifetime reproduction, because of their high ability for compensatory growth (Zedrosser et al. 2013). The differences in diet, physiology, and timing and chronology of life history events suggest that food variation could have different implications for a large-bodied omnivorous hibernator than obligate herbivores.

Bilberry *Vaccinium myrtillus*, lingonberry *V. vitis-idaea* and crowberry *Empetrum hermaphroditum* are the most important food resources for bears in Scandinavia during hyperphagia (Stenset et al. 2016). Peak fruit production of berries follows regular masting cycles of 2–5 years (Selås 2000) that are altered by weather conditions during crucial stages of berry phenology (Selås 2000, Bokhorst et al. 2011, Rixen et al. 2012, Selås et al. 2015). Masting describes the phenomenon that seed production, and thereby the production of fruits, fluctuates between years in a synchronized fashion across plants in a population (Silvertown 1980). The emergence of masting cycles has been ascribed to resource limitations and weather cues (Kelly et al. 2013, Pearse et al. 2016) and can be additionally modified by weather during plant phenology, flowering, and fruit ripening (Kelly and Sork 2002). Bilberry, for example, needs a stable insulating snow cover during winter and berry production is sensitive to cold temperatures during flowering (around May in Scandinavia), drought stress during fruit ripening (June– July), and high temperatures during bud formation in autumn (August–September) (Selås 2000, Selås et al. 2015). Recent experimental and observational studies from northern Sweden have found evidence that late winter warming events may reduce bilberry production by up to 95% (Bokhorst et al. 2008, 2011). Fewer studies have described the role of climatic events on fruit production of lingonberry, supposedly due to their lower economic value (but see Bokhorst et al. 2008, 2010).

Our objective was to quantify interannual variation in bear food abundance during hyperphagia to 1) evaluate to what extent climatic events during key stages of berry plant phenology synchronize fruit production, 2) determine whether fruit production varies among sampling years in a synchronized fashion, and if so, 3) quantify the effects of varying fruit production on life history traits of brown bears. We modeled food availability as fruit abundance of bilberry and lingonberry. We built models to test competing hypotheses proposed for how weather modulates berry production for both species in Scandinavia (Supplementary material Appendix 1 Table A1). We then analyzed whether interannual variation in bilberry and lingonberry abundance could explain variation in brown bear life history traits in our study population, i.e. autumn mass of hunter-killed females, spring mass of yearlings, and female reproductive success (implantation and early cub survival). Bears are hunted at the peak of the bilberry season and before the lingonberry season in autumn (Bischof et al. 2009) and we expected killed bears to be heavier when bilberry abundance was high. We expected spring mass of yearlings to be higher when either bilberry or lingonberry was plentiful in the preceding autumn. Lastly,

we predicted that female reproductive success would be lower after years of simultaneous failure of lingonberry and bilberry and hypothesized that body mass at the beginning of hyperphagia may buffer this effect. Unifying these three components, our overarching hypothesis was, therefore, that weather events affect bilberry and lingonberry abundance, and, if synchronized, they indirectly affect bear life history.

Methods

Study areas

Berry abundance was measured at the Siljansfors Experimental Forest in Dalarna (60°89′N, 14°38′E, Fig. 1a). The bear study area was located in the counties of Dalarna and Gävleborg in central Sweden (approximately 61°5′N, 15°05′E, Fig. 1a), about 40 km northeast of the Siljansfors Experimental Forest. Landscape parameters, forestry practices, and weather were similar in both areas.

Berry data

For both bilberry and lingonberry, we selected permanent berry monitoring plots sampled over ten continuous years (2006–2015) in six forest stands representative for the area; two each in young forests, thinned forests, and mature forests (Supplementary material Appendix 2 Fig. A1). Change in canopy cover over the study period was not recorded but all stands were relatively open with only little expected change in canopy cover over the study period. In each stand type, ten (nine from 2009 onwards) 0.25 m² circular plots were established in a circular design 10 m from each other (Supplementary material Appendix 2 Fig. A2). The total number of sampling plots and assessment events was 558 for each species (n = 60 annually in 2006–2008; n = 54 annually in 2009–2015). Ripe bilberries were counted between late July and late August and ripe lingonberries between late August and mid-September, with a small annual variation depending on the annual berry ripening phenology. To facilitate interpretation, we calculated the number of berries per m².
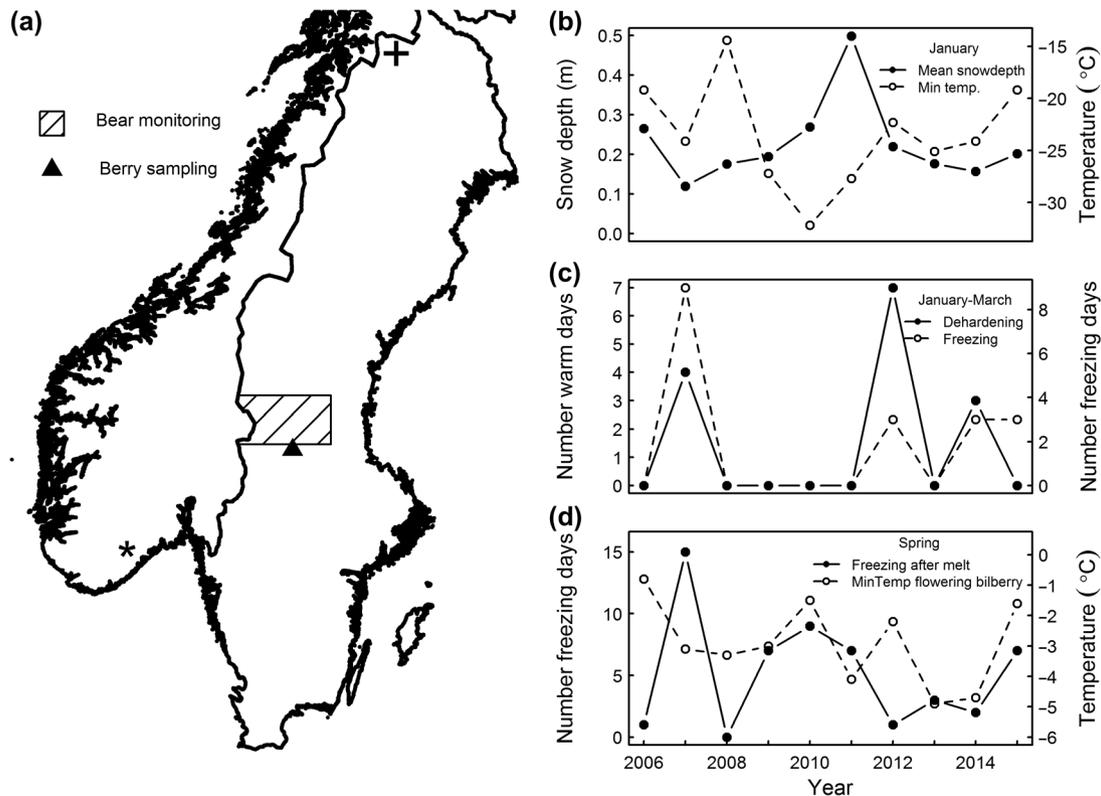

Figure 1. Locations of the study areas in Scandinavia (a) and annually explicit, discrete weather covariates recorded at the berry monitoring site (b–d). Permanent berry monitoring plots were obtained from the Swedish University of Agricultural Sciences experimental forest in Siljansfors (black triangle panel a). The area of intensive bear monitoring (hatched area panel a) lies slightly north of the berry sampling area. Locations where two of the referenced berry studies had taken place are indicated by + for Abisko, Sweden (Bokhorst et al. 2011) and * for Vest-Agder, Norway (Selås 2000, Selås et al. 2015). (b) mean January temperature (dashed line) and snow depth (solid line); (c) number of days with warm temperatures (maximum daily temperature > 4°C) and no snow cover (dehardening, solid line) and freezing temperatures (minimum temperature < –1°C) and no snow cover (freezing, dashed line) from January until March; (d) number of freezing days later than 14 days after snow melt when plant phenology has been induced (solid line) and minimum temperature in May (dashed line). Temperature was recorded at Siljansfors between 2006 and 2014. Snow depth was extracted from extrapolated snow cover data from weather stations in the surrounding of the berry monitoring site.

Interannual variation of berry production

To obtain an index of annual berry production that was independent of forest stand characteristics, which are important drivers of the variation in berry production (Hertel et al. 2016), we used the annual number of berries in a given plot minus the 10-year average number of berries in that plot. Positive values (i.e. deviations) indicated above-average and negative values below-average berry abundance for a given year in a given plot. We used these plot-specific deviations as response variables in a set of seven competing linear mixed effects models to identify the most important drivers of interannual variation in berry production (Supplementary material Appendix 1 Table A1). We analyzed production of bilberry and lingonberry separately.

Weather events affecting berry production

For models evaluating the effect of weather on berry production, we obtained daily minimum, maximum, and mean temperature (°C) and precipitation (mm), all recorded at a height of 1.7 m at the Siljansfors Experimental Forest weather station. Snow depth was measured on only 14 days per year, which was not fine-scaled enough to identify short-term snowmelt events. We therefore obtained local measures of snow depth (m) from 321 weather stations (Swedish Meterological and Hydrological Inst.) surrounding the experimental forest. Station-specific time series of snow depth within the study area were converted to interpolated raster series (1985–2014; 5-day temporal resolution; 5 km spatial resolution) using the R package MBA (Finley and Banerjee 2014). Time series of snow depth were then extracted from these rasters for the weather station in the Experimental Forest. To evaluate the validity of predicted snow depths, we correlated extracted and observed snow depths at the Siljansfors weather station using 140 measurement days between 2005 and 2015 (Pearson correlation, $r = 0.927$ Supplementary material Appendix 2 Fig. A3). From the daily weather data, we extracted covariates that have been reported to affect berry productivity in the literature (Supplementary material Appendix 1 Table A1). Besides monthly averages and minima temperature and snow depth, we also extracted the number of growing degree days (Rixen et al. 2012) and whether plants were subject to dehardening or freezing damage between January and March (Bokhorst et al. 2011) or to freezing damage after snow melt (Rixen et al. 2012). We also formulated an expert model for our study system. To more closely match climate events to the period of phenological events, we determined the period of flowering for bilberry and lingonberry for each year. Phenology data were obtained from the Siljansfors Experimental Forest (Supplementary material Appendix 2 Fig. A4). We extracted the minimum temperature during each annually explicit period of flowering of bilberry and lingonberry. We selected the most influential weather covariates used in the literature-based candidate models by examining whether their estimates overlapped with zero. We also formulated a

model testing the ΔT hypothesis that masting is driven by the temperature difference between the two preceding summers (Kelly et al. 2013). Refer to Supplementary material Appendix 1 Table A1 for definitions of model covariates. Lastly, we formulated an intercept-only model, representing the case where interannual variation in berry production was absent. We fitted linear mixed effect models with a random intercept for plot ID, nested within forest stand ($n = 6$), nested within forest stand type ($n = 3$). We assessed multicollinearity of predictor variables entered into the same candidate model by examining correlation coefficients. If predictors were correlated > 0.6 we only retained the predictor which affected berry abundance more strongly in the model. We compared alternative models with the AIC model selection criterion (Supplementary material Appendix 1 Table A1), based on maximum likelihood (Zuur et al. 2009).

Berry production index

To relate observed berry production to bear life history traits, we formulated a model explaining berry production with study year as a fixed effect. For both berry species, we predicted the deviation from the mean number of berries for every monitoring year with method type set to restricted maximum likelihood (Zuur et al. 2009). The resulting index was then scaled between 0 and 1 and used as an annual index of bilberry and lingonberry abundance.

Female autumn body mass

We used body mass data from 291 female bears harvested in our study area in the counties of Dalarna and Gävleborg in the first 4 weeks of the annual bear hunting season between 2006 and 2015, obtained from the National Veterinary Inst. of Sweden. All bears that are legally harvested during the hunting season (lasting from 21 August 21 until the quota is filled, latest 15 October) are weighed by an officially appointed inspector on the day of harvest (Bischof et al. 2009). Ages were determined by counting tooth cementum annuli. We fitted linear regression models explaining autumn mass with age, bilberry index, lingonberry index, and their interactions as explanatory variables (Table 1). We tested a priori for nonlinear relationships for both age and bilberry index with autumn mass.

Yearling spring body mass

We used the body mass of all yearlings ($n = 132$, 59 females, 73 males) captured in April or May 2007–2016 as part of an individual-based long-term research program (Zedrosser et al. 2006, 2013). We fitted a linear mixed effects model on yearling body mass using either an interaction between the bilberry and lingonberry index, an additive effect, or the two berry indices separately as predictors of yearling body mass (Table 1). We tested a priori for a nonlinear relationship between food abundance and the response yearling body

Table 1. Model selection results evaluating food abundance effects on bear life history traits. Autumn body mass was collected from female bears which were killed by hunters in and around the study area of the Scandinavian bear project in central Sweden during the annual bear hunting season between 2006–2015. Yearling spring body mass and female reproductive success were collected from marked bears within the study area of the Scandinavian bear project (Fig. 1A) between 2007–2016. We test for the effects of both bilberry and lingonberry abundance, as well as winter severity on spring traits. Continuous variables that were part of an interaction were standardized by subtracting the mean and dividing by the standard deviation. The most parsimonious models are highlighted in bold.

Trait	Candidate model	df	ΔAIC	Akaike weight
Female autumn body mass	BilIndex × poly(Age,3)	9	0	0.55
	BilIndex + poly(Age,3)	**6**	**0.92**	**0.26**
	BilIndex × LingIndex + poly(Age,3)	8	4.07	0.06
	BilIndex + LingIndex + poly(Age,3)	7	2.46	0.10
	poly(Age,3)	5	4.91	0.03
	1	2	327.48	0.00
Yearling spring body mass	BilIndex × LingIndex + MotherMass + Sex + Littersize + WinterSeverityIndex	11	3.63	0.05
	BilIndex × LingIndex + MotherMass + Sex + Littersize	10	1.04	0.16
	BilIndex × MotherMass + LingIndex + Sex + Littersize + WinterSeverityIndex	11	1.91	0.11
	BilIndex × MotherMass + LingIndex + Sex + Littersize	10	0.13	0.26
	BilIndex + MotherMass + Sex + Littersize + WinterSeverityIndex	9	1.56	0.12
	BilIndex + MotherMass + Sex + Littersize	**8**	**0**	**0.28**
	LingIndex + MotherMass + Sex + Littersize + WinterSeverityIndex	9	5.39	0.02
	LingIndex + MotherMass + Sex + Littersize	8	9.87	0.00
	MotherMass + Sex + Littersize	7	7.88	0.00
	1	3	47.85	0.00
Female reproductive success	BilIndex × SpringMass$_{t-1}$ + LingIndex + WinterSeverityIndex	6	3.27	0.08
	BilIndex × SpringMass$_{t-1}$ + LingIndex	5	1.81	0.18
	BilIndex × SpringMass$_{t-1}$ + WinterSeverityIndex	5	1.43	0.21
	BilIndex × SpringMass$_{t-1}$	**4**	**0.00**	**0.44**
	BilIndex + SpringMass$_{t-1}$ + LingIndex + WinterSeverityIndex	5	9.52	0.00
	BilIndex + SpringMass$_{t-1}$ + LingIndex	4	8.04	0.01
	BilIndex + SpringMass$_{t-1}$ + WinterSeverityIndex	4	7.67	0.01
	BilIndex + SpringMass$_{t-1}$	3	6.13	0.02
	SpringMass$_{t-1}$	2	4.61	0.04
	1	1	16.43	0.00

mass and for an additive effect of winter severity (number of days between November and April with temperatures below –10°C). Body mass of the mother, number (litter size), and sex of siblings affect body mass of yearlings (Zedrosser et al. 2006) and thus were controlled for in the model. Litter ID was fitted as a random effect to account for nonindependence among litter mates.

Female reproductive success

We used data on the reproductive success of 36 females between 2007–2016 (74 bear years). In our study population, primiparity occurs at 4 to 6 years of age (Zedrosser et al. 2009), when females have reached 84% of their asymptotic body mass (Scandinavia Brown Bear Research Project, unpublished data, Supplementary material Appendix 2 Fig. A6). We included all female bears aged 6 or older in our study. Bears were weighed in a sling suspended beneath a spring scale in spring or early summer before the start of the berry season (15 July). Loss of cubs-of-the-year after 1 May is almost always due to infanticide (Steyaert et al. 2012, 2013), whereas cub loss before May can be attributed to poor nutritional conditions (Zedrosser et al. 2009). We classified females as successfully reproducing when their cubs-of-the-year survived longer than 1 May. Unsuccessful females were those that gave birth, but lost cubs before

1 May and females that were available for reproduction, but did not produce cubs. We used a binomial generalized linear model to evaluate the effects of the variables food availability in autumn (bilberry and lingonberry indices), winter severity, and body mass prior to hyperphagia (Table 1) on reproductive success (successful versus unsuccessful reproduction). To allow for a differential effect of food abundance on reproductive success, depending on initial body mass, spring body mass in the berry year (i.e. the year before reproductive success was determined) was fitted as an additive effect or as part of an interaction with food availability (Table 1). We tested a priori for nonlinear effects of food abundance on reproductive success by comparing models including the berry indices as linear, second order, or third order polynomials.

We prepared the data and fit statistical models in R using the package *nlme* (Pinheiro et al. 2013) for linear mixed effect models. Continuous variables were standardized by subtracting the mean and dividing by the standard deviation. For model selection, the argument method was set to maximum likelihood and for predictions and model interpretation, argument was set to restricted maximum likelihood (Zuur et al. 2009). Model selection was carried out according to Burnham and Anderson (2002); we selected the simplest model within an AIC ≤ 2 of the model with the lowest AIC value. We inspected diagnostic plots to validate model assumptions.

Data deposition

Results

Interannual variation in berry production

The mean annual number of berries for all plots was 70 bilberries m^{-2} (min 3, 1st quartile 25, median 52, 2nd quartile 98, max 258 bilberries) and 100 lingonberries m^{-2} (min 0, 1st quartile 16, median 35, 2nd quartile 98, max 726 lingonberries).

Weather events affecting berry production

For bilberry, the expert model outperformed all other candidate models (Supplementary material Appendix 1 Table A1). Bilberry production was higher when January temperatures were warmer, irrespective of snow depth (Fig. 2). Lower minimum temperatures during flowering (Fig. 2) had a significant negative effect on bilberry production. Rainy summers (Fig. 2) had a negative effect on bilberry production, and a longer growing season (not shown) had a positive effect on bilberry production (significance was determined from examining the overlap of 95% confidence intervals with 0, Supplementary material Appendix 2 Fig. A7). For lingonberry, higher April snow depth, higher May temperature, and higher temperature during fruit ripening in the preceding year led to higher lingonberry production

(Fig. 2, Supplementary material Appendix 2 Fig. A7). However, weather covariates explained little of the variation in berry production (R^2 expert model bilberry = 9.5%, R^2 Selås et al. 2015 model lingonberry = 11.7%).

Interannual variation of key weather covariates was moderate and generally nonsynchronous (Fig. 1b–d, Supplementary material Appendix 2 Fig. A5). Average January snow depth ranged between 12 and 50 cm, and average January temperature was coldest in 2010 (–15°) and warmest in 2008 (–1.4°) (Fig. 1b). Winter thaws and freezing events were observed in the winters of 2007, 2012, 2014 and 2015 (Fig. 1c). In summary, the variables describing winter severity in the different candidate models did not point towards one or several years of extreme climatic events or winter severity. The minimum temperature during flowering of bilberry but not lingonberry dropped below freezing at least once in all years (Fig. 1d, Supplementary material Appendix 2 Fig. A5). The number of freezing days after snowmelt in spring i.e. during plant phenology varied between 0 and 15 (Fig. 1d), and 2015, the year with the highest berry production, had the coldest average May temperature (Supplementary material Appendix 2 Fig. A5).

Berry production index

For both bilberries and lingonberries, a year-effect model (R^2 year effect model bilberry = 11%, R^2 year effect model lingonberry = 15%) outcompeted the intercept-only models (bilberry ΔAIC = 48, lingonberry ΔAIC = 73) and the most parsimonious weather-effect model (bilberry ΔAIC = 3, lingonberry ΔAIC = 17). This means that the
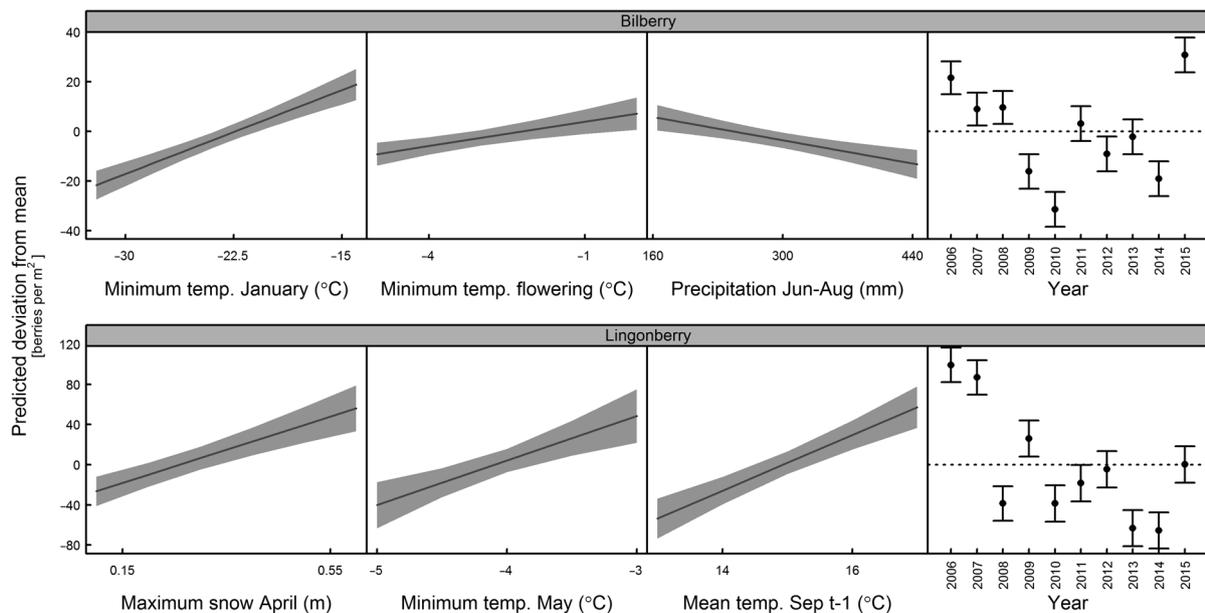

Figure 2. Predicted deviation from the mean number of berries (± SE) per square meter as a function of influential weather covariates from the most parsimonious weather effects model (first three columns), and predicted annual deviation. Effects were calculated from 60 (from 2009 onwards 54) m^2 plots which were repeatedly sampled between 2006–2015 at the Siljansfors Experimental Forest in central Sweden. Effects on bilberry production are shown in the top row, effects on lingonberry production in the bottom row.

annual deviation of bilberries and lingonberries varied among years in a synchronous manner across all plots (for model coefficients see Supplementary material Appendix 2 Fig. A8). The annual deviation from the mean fluctuated more strongly for lingonberry than for bilberry (Fig. 2). Bilberry produced a predicted 30 ± 7 (mean $\pm$ SE) more berries per m^2 than the overall mean in the best production year (2015), as opposed to 31 ± 7 (mean $\pm$ SE) fewer berries in the worst year (2010). Lingonberry produced between 99 ± 17 (mean $\pm$ SE) more and 65 ± 17 (mean $\pm$ SE) fewer berries, in 2006 and 2014 respectively. The occurrence of very good and very bad production was not synchronized for the two species.

Female autumn body mass

Autumn body mass of harvested solitary female bears increased linearly with increasing bilberry abundance, but not lingonberry abundance. Females weighed approximately 10 kg less in the year of lowest bilberry abundance than in that of highest bilberry abundance (Fig. 3a). The food-body mass relationship was not explained better by including interactive effects with the age of the female. This indicates that food effects on body mass were of a similar magnitude, regardless of a bear's age. Because a third-order polynomial performed best in approximating the intrinsic age–body mass relationship and female growth curves reached an asymptote at approximately 5-6 years of age (Supplementary material Appendix 2 Fig. A6), the relative food effect on the body mass of growing females was stronger. As an example, the relative mass difference between the years of highest and lowest food abundance was 13% for a two-year-old, 9% for a four-year-old, and 7% for a fully grown 8-year-old female. Coefficients of the best performing model are provided in Supplementary material Appendix 2 Fig. A9.

Yearling spring body mass

Yearling body mass varied linearly in response to annual bilberry abundance (Table 1). Yearlings were lighter when bilberry abundance had been low in the previous autumn and heavier when it had been very high (Fig. 3b). The mother's body mass, yearling's sex, and litter size were significant covariates, as has been shown previously in the same population (Zedrosser et al. 2006). Yearlings were heavier when born to a heavier mother, when being the only cub as compared to litters of two or three, and when being male as compared to female. Body mass was affected at a relevant scale by bilberry abundance, yearlings weighed an estimated 4.12 kg less in the worst bilberry year as opposed to the best one. For a female cub born into a litter of two and to a mother of average body mass (Fig. 3b), this translates into a 21% lower body mass. Lingonberry abundance and winter severity did not affect yearling body mass significantly (0 was contained within the 95% confidence interval). See Supplementary material Appendix 2 Fig. A9 for an overview of model coefficients.
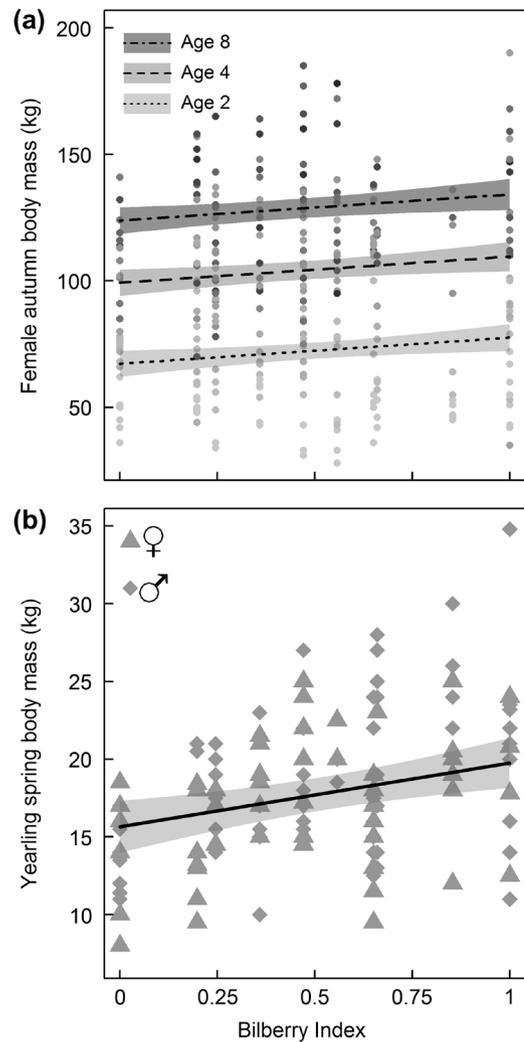

Figure 3. Predicted autumn body mass of female brown bears (a) and predicted spring yearling body mass (b) along a gradient of bilberry abundance. Autumn body masses (a) were obtained from female bears killed by hunters during the annual bear hunting season 2006–2015 in and around the study area of the Scandinavian bear project in central Sweden. Observed female autumn body masses are shown in filled dots colored according to age of the bear with younger bears in lighter and older bears in darker shades of gray. Estimates are exemplary shown for a 2-, 4- and 8-year-old female. Yearling masses (b) were obtained from bears captured by the Scandinavian bear project in spring 2007–2016. Observed yearling body masses are shown in triangles for females and in diamonds for males. Estimates are shown for a female yearling, born into a litter of two with a mother of average body mass. Shaded areas present 95% confidence intervals.

Reproductive success

Bilberry abundance differentially affected a female's probability to reproduce depending on her body mass in the preceding spring (Fig. 4, Supplementary material Appendix 2 Fig. A9). Spring body mass ranged between 47 and 120 kg (mean $\pm$ SD: 80 ± 16) and lighter females had a lower probability to reproduce when autumn bilberry abundance
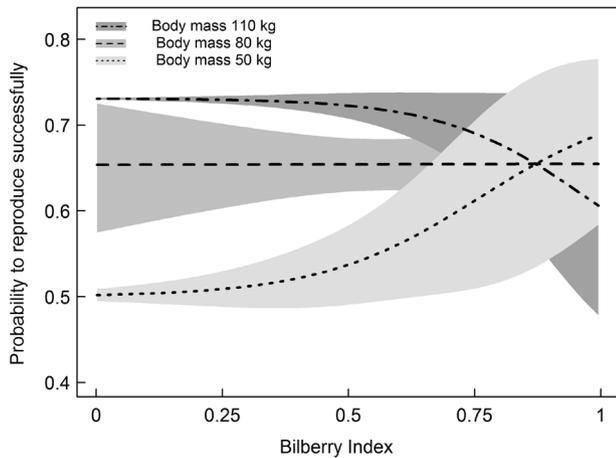
Figure 4. Predicted probability that a female brown bear will reproduce successfully along the gradient of bilberry abundance during hyperphagia in autumn. Estimates are shown for females of average (80 kg), low (50 kg) and high (110 kg) body mass in the preceding spring. Shaded areas show 95% confidence intervals.

was lower than average, compared to females of average or high spring body mass. When bilberry abundance was high, however, their probability to reproduce successfully did not differ from heavier females. Autumn bilberry abundance neither increased nor decreased a female's probability to reproduce if she already had an average or above-average body mass in spring. Wide confidence intervals indicated limited inference at high bilberry abundances. The predicted decrease in reproductive success for heavy females at high bilberry abundance is therefore a mathematical artifact.

Discussion

The overwhelming majority of literature on indirect climate effects on mammals via direct effects on plants concentrates on winter conditions (Jacobson et al. 2004, Portier et al. 1998) or on how changes in spring green-up phenology affect fitness measures in obligate herbivorous ruminants (Post and Stenseth 1999, Burthe et al. 2011, Tveraa et al. 2013) and rodents (Réale et al. 2003, Ozgul et al. 2010). To date there is limited information on how climate affects omnivores that rely on higher-quality plant forage, such as berries, and for a limited period of time (but see McLellan and Hovey 1995, McLellan 2011, 2015). We found that berry production over a 10-year period was affected by weather during plant phenology, berry flowering, and ripening. Berry production was favored by mild temperatures in January and during flowering, by low amounts of precipitation during berry ripening, and by a longer growing season. Bear life history traits were correlated with fluctuations in the abundance of berries between years. However, only bilberry, and not lingonberry fluctuations drove variation in body mass and reproductive success of Scandinavian brown bears, even though the two

berry species may serve as complementary food resources (Hertel et al. 2016, Stenset et al. 2016). This highlights the vulnerability of bears facing global changes, if reproductive success depends so much on a single berry species.

A direct link between bilberry abundance and body mass

Autumn bilberry abundance positively affected the autumn body mass of single female bears in a similar linear fashion across all ages. Likewise, spring body mass of yearlings increased with increasing bilberry abundance prior to hibernation. Also, the mother's body mass upon den emergence affected yearling body mass positively, indicating that cubs profited from a mother that had found good foraging areas in autumn and left the den in better-than-average condition herself. These results are consistent with findings from North America, where food supply has been directly linked to American black bear *Ursus americanus* cub growth in the first year (Jonkel 1971, Rogers 1976).

Initial body mass and food determine reproduction

Low bilberry abundance reduced the reproductive success of females that started autumn hyperphagia in a poorer-than-average body mass. However, when berry production was above average, lightweight females were able to compensate for their poor body condition and increase their likelihood to reproduce to the same level as females with average or better-than-average spring body mass. Bilberry abundance did not affect the likelihood to reproduce for females that entered hyperphagia with an average body mass. The measure of uncertainty around the model estimates increased at higher bilberry abundances, suggesting that when food was not limiting, factors unrelated to nutrition (e.g. social factors, Ordiz et al. 2008, or density dependence, Zedrosser et al. 2006) became more important in determining reproductive success. Bears need a minimum of 19% body fat to support reproduction and lactation (López-Alfaro et al. 2013). Our results suggested that females that entered the berry season with a low body mass were not able to reach that threshold in years of low food abundance and either did not implant their blastocytes or lost their cubs at a very early stage due to insufficient lactation.

Link between berry production and measured weather variables

Using 10 years of accurate, on-site temperature, precipitation, and snow measurements, we could identify weather covariates affecting variation in berry production. A priori data exploration and matching periods of freezing in spring in relation to when plants were indeed flowering, rather than a preset time period, revealed the best model fit for bilberry. Bilberry produced better after mild winters, regardless of snow cover. This is in contrast to our expectations from the Bokhorst et al. (2011) and Selås (2000)

candidate models, and results elsewhere (Ögren 1996). In their 2015 study however, Selås et al. could not confirm an effect of winter temperature and/or snow accumulation on bilberry production. These opposing findings indicate that the effects of mild winters on bilberry production are still obscure. We suggest that local environmental conditions may further alter this relationship. For example, neither our findings, nor studies by Selås (2000) and Selås et al. (2015) explicitly tested interactive effects between weather covariates and forest stand characteristics (Kardell 1979, Hertel et al. 2016). Older forests buffer temperature variation more than more open habitats, like clearcuts, where temperature amplitudes are higher (Pigeon et al. 2016, Supplementary material Appendix 2 Fig. A10). Snow cover on clearcuts is exposed to direct sun incidence and wind drift and therefore varies more, which readily exposes berry plants there to ambient temperatures. The 'conditions' on clearcuts may therefore resemble those of open arctic tundra (asterisk in Fig. 1a), where winter variability adversely affected bilberry production (Bokhorst et al. 2011). For lingonberry, we found that increasing snow cover in April positively affected berry production, most likely because late snow delays flowering, thereby reducing the risk of freezing during flowering (Selås et al. 2015). Under future climate scenarios (ACIA 2005), winters in Scandinavia are expected to become milder. It remains to be seen how this will affect berry production.

On a less ambiguous note, we found berry production of both species to be negatively affected by cold temperatures during flowering, which is in line with predictions from Selås (2000) and Selås et al. (2015). However for bilberry this effect was only apparent when matching temperature quantification to the exact time of flowering. The scale at which to measure climate in space and time and the composition of different weather variables present considerable challenges in ecology (Stenseth and Mysterud 2005). We show that explicitly matching measurement time scales can reveal relationships that otherwise go undetected. The frequency of frosts after snow melt may increase in the future with advances in the date of snowmelt (Rixen et al. 2012, Wheeler et al. 2014), posing a potential threat to future berry production. Selås (2000) reported low bilberry production in dry summers. Amounts of precipitation in our study were similar (range 160–440 mm) to those reported by Selås (2000; Fig. 4 range: 100–550 mm), but we found a reversed effect, that high amounts of precipitation were detrimental to berry production. Longer summers, measured as growing degree days, had a positive effect on bilberry production and high temperatures during the preceding berry season had a positive effect on lingonberry production. Summers in Scandinavia are expected to become warmer and wetter in the future (ACIA 2005), which could lead to interactive effects on berry production. We did not find evidence supporting the ΔT hypothesis that temperature difference between the two preceding years drives masting cycles (Kelly et al. 2013).

Life history responses of bears compared to ungulates

In contrast to bears, herbivores, for example roe deer *Capreolus capreolus*, have extremely high adult conception rates, food effects on adult female reproduction are weak, and winter body mass only affects pregnancy in primiparous females (Gaillard et al. 1992). However, offspring mass and their survival and fecundity as adults are strongly affected by conditions early in life (Gaillard et al. 1992, 1998, Pettorelli et al. 2007), such as harsh winter conditions when fawns are in utero (Forchhammer et al. 2001) and mismatch with highly nutritious vegetation at fawning (Pettorelli et al. 2007). Cohort effects of conditions early in life are therefore strong drivers of population dynamics in ruminants (Albon et al. 1987, Couturier et al. 2009). Bears however have a different timing of life history events and physiological adaptations than large herbivores. Bears give birth during hibernation when neither the female nor the offspring have access to food; cub production and early cub survival depend on the female's fat reserves accumulated during the active season (López-Alfaro et al. 2013). Furthermore, bears cope with intra-annual body mass fluctuations of up to 65% (Swenson et al. 2007), with a minimum mass in spring after den emergence and a maximum mass in autumn at the end of hyperphagia. The prerequisite for these extreme weight gains and losses within the course of a few months is that bears can exploit short-term, highly abundant food through rapid compensatory mass gain. This also explains why mass as a yearling does not affect life time reproductive success in bears (Zedrosser et al. 2013). Intake rate is the prime limitation for mass gain in frugivorous bear populations (Welch et al. 1997) and in our study bears of all ages were lighter in years of lower fruit abundance.

Conclusion

We found consistent evidence from three independent life history measures for bottom–up limiting effects of one key food resource on a large-bodied omnivorous hibernator. Our strong evidence is surprising, given that bears have the digestive capacity and behavioral plasticity to fall back on other food resources when one is scarce (Beckmann and Berger 2003). Linking bilberry abundance to local weather events, we found that berry production was depressed in wet summers, and summer precipitation is expected to increase in the future. Conversely, increasingly warm winters, springs, and longer summers may favor bilberry production in the future.

There are indeed very few climate effects studies focusing on fall phenology and their drivers (Gallinat et al. 2015). Fruits, nuts and berries can be considered as «energy bombs» compared to other forage, in particular at a time of year when green leaves are dying. Masting of acorns drives population cycles of rodents in USA (Ostfeld et al. 2006) and hoarding by seed-eating birds (Pesendorfer and Koenig 2016), while masting of oak seed affected recruitment in European bison (Mysterud et al. 2007). Fall phenology is hence affecting

a wide range of herbivores and omnivores and thereby ecosystem process (Ostfeld et al. 2006) and clearly warrants further attention.

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