A framework for reproductive outcomes of phenological match-mismatch in migratory breeders tested on a declining species, caribou

Eric Post[1]*, Pernille Sporon Bøving[1], R. Conor Higgins[2], Christian John[3], Mason Post[4], Bradyn O'Connor[1], Jesika P. Reimer[1], Nikki Williamson[1], and Jeffrey T. Kerby[5]

[1]Department of Wildlife, Fish, & Conservation Biology, University of California, Davis, 95616 USA
[2]Yolo County Resource Conservation District, 221 W Court St., Suite 1, Woodland, CA 95695, USA
[3]Marine Science Institute, University of California, Santa Barbara, CA 93106, USA
[4]Brotman Baty Institute, University of Washington, Seattle, WA 98195, USA
[5]Scott Polar Research Institute, Department of Geography, University of Cambridge CB2 1ER, UK

*corresponding author: Eric Post

Email: post@ucdavis.edu

Author Contributions:
Conceptualization: EP, PSB, CJ, JTK
Data Curation: EP, PSB, RCH, CJ, BO, JPR, NW, JTK
Formal Analysis: EP
Funding Acquisition: EP, PSB, JTK
Investigation: EP, PSB, RCH, CJ, MP, BO, JPR, NW, JTK
Methodology: EP, RCH, CJ, MP, JPR, JTK
Project Administration: EP, PSB, JTK
Resources: EP, JTK
Supervision: EP, JTK
Validation: EP, JTK
Visualization: EP
Writing - Original Draft Preparation: EP
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Abstract

Long distance migrants with endogenously timed reproduction may be especially vulnerable to phenological mismatch on summer ranges where offspring are produced and provisioned. This is because departure timing from winter ranges and breeding timing on summer ranges in such species is cued primarily by photoperiod while the timing of resource availability on summer ranges is cued by local temperature. Hence, studies of climate change driven mismatch have focused nearly exclusively on one aspect of resource phenology: the timing of resource availability on summer ranges. Here we present a predictive framework for reproductive outcomes in long-distance migrants that integrates the seasonal timing and rate of increase in resource availability on summer ranges. The framework predicts that potential disadvantages of early resource availability relative to resource demand may be buffered by slow rates of increase in seasonal resource availability. Conversely, potential advantages of later resource availability that coincides with the timing of resource demand may be unrealized if resource availability increases too rapidly. We test the framework using 21 years of offspring production by tundra caribou, a long-distance migratory breeder whose global abundance is in decline, whose timing of reproduction is endogenously entrained, and for whom resource availability on summer ranges may advance with local warming. Agreement with empirical outcomes for caribou in this case study suggests broader utility of this framework for predicting climate change consequences for phenological match-mismatch in other long distance migratory breeders.

Main Text

Introduction

Evidence from a diverse array of species and systems indicates that climate change can disrupt synchrony between the seasonal timing of resource demand and availability for consumers, with adverse consequences for consumer productivity (1-8). Such disruption may arise through two pathways. In one, the seasonal timing of activity of species in adjacent trophic levels within the same system may be differentially responsive to interannual variability or trends in shared abiotic cues such as temperature (3). Alternatively, the seasonal timing of activity of species in adjacent trophic levels may be cued by different factors entirely (9). In the former case, phenological or trophic mismatch may occur if warming-related rates of advance in the timing of offspring production and resource demand by consumers do not keep pace with warming-related rates of advance in the seasonal timing of availability of resource species used by consumers to provision offspring (10). In the latter case, phenological mismatch may develop if the seasonal timing of offspring production by consumers is entrained by factors that do not change with warming while the seasonal timing of availability of resource species used by consumers advances with warming (11). This latter scenario may be more likely to develop with climate change in long-distance migratory breeders whose seasonal reproductive timing, including departure for summer ranges, is circannually entrained and cued by photoperiod (12-14). While such species may be able to adjust timing of arrival at summer ranges in response to variation in resource phenology in transit (15, 16), timing of breeding and hence of offspring production itself may be less sensitive to warming and therefore lag advances in resource phenology where offspring are produced and must be provisioned (9, 17).

Because of the critical importance of synchrony inherent to consumer-resource dynamics in such scenarios, efforts to test the predictions of phenological match-mismatch hypotheses with respect to the consequences of climate change conventionally focus on changes in timing of resource demand relative to resource availability (18-20). The availability of resources may, however, vary not only in timing but also in rate at which availability increases in response to warming (21, 22). The rate of springtime green-up of vegetation, an important resource for herbivores with distinct annual breeding cycles, has, for example, accelerated with warming over the past three decades in northern high latitudes (23). Interactions between the timing and rate of increase in resource availability are expected to have important demographic consequences for phenological match and mismatch between consumer and resource species (22). For instance, under certain conditions such interactions may enable long-distance migratory breeders to compensate, at least partially, for potentially mismatched timing due to advancing resource availability under climate change (22). Conversely, the interaction between timing and rate of increase in resource availability may, under other circumstances, constrain or even nullify presumed advantages of matched timing for consumers. We elaborate this proposition by presenting a framework that predicts outcomes for consumer productivity of interactions between the timing and rate of increase in seasonal resource availability for long-distance migratory breeders. The framework is intended to add nuance to considerations of consequences for consumer productivity not presently considered under the conventional phenological match-mismatch concept. We then test predictions of this framework using long-term data on timing and magnitude of offspring production by tundra caribou (*Rangifer tarandus*), a long-distance migratory breeder in decline across much of the Arctic (24, 25).

The framework

The predictive framework presented here applies elements of the classic trophic match-mismatch hypothesis (19, 26) while relaxing some of its conditions. For instance, we assume that the consumer species experiences a critical phase in its annual life cycle, in this case the timing of offspring production. However, recognizing that critical tests of the match-mismatch hypothesis using field-derived demographic data may not meet all of the formal assumptions of the hypothesis (20), our framework does not predict outcomes for fitness of individual consumers. Rather, we focus on outcomes for more readily observed and quantifiable metrics such as the number of offspring produced per female at the population level in a breeding season. We also assume the availability of sufficient information to characterize conditions on seasonal ranges where offspring are produced (i.e., springtime conditions) relative to some baseline (20) and hence acknowledge that application of this framework may necessitate existence of relatively long-term multi-annual data. Finally, we assume the consistent availability of intra-seasonal data for use in estimating the annual rate of increase in resource availability for each (or most) years for which annual timing of resource availability on summer ranges is quantified.

Given these caveats, we propose categorization of the resource state for consumer provisioning of offspring as follows. The annual timing of resource availability may be early or late relative to the timing of resource demand by consumers for offspring production and provisioning (Figure 1a, left panels). Similarly, the seasonal rate of increase in availability of resources used by consumers to support the costs of offspring production and provisioning may be rapid or slow (Figure 1a, right panels). Because this framework is intended to apply to reproductive outcomes for long-distance migratory breeders with strong circannual (i.e., endogenous) regulation of the timing of reproduction it predicts that earlier resource availability and faster increases in resource availability will have adverse consequences for consumers (Figure 1a, purple panels). In contrast, later resource availability and slower increases in resource availability should have beneficial consequences for consumer productivity (Figure 1a, green panels).

Interactions between timing and rate of increase in resource availability under this framework hence allow for more nuanced predictions of reproductive outcomes for consumers than is possible under considerations of the relative timing of resource availability alone [*sensu* (21)]. For instance, while earlier resource availability may be disadvantageous for consumers, slower increases in resource availability in early springs should be less disadvantageous because such conditions may prolong opportunities for offspring provisioning (Figure 1b, gray). In contrast, while later resource availability should be advantageous, any benefits accruing in later springs may be constrained or even offset if the rate of increase in resource availability is also rapid, thereby truncating offspring provisioning (Figure 1b, gray). Finally, the most disadvantageous conditions for consumer productivity are to be expected in early springs with rapid increases in resource availability (Figure 1b, dark purple) while the most advantageous conditions are expected in late springs with slow increases in resource availability (Figure 1b, dark green), provided these conditions do not place the timing of resource availability beyond the critical period. When these conditions apply, the framework thus predicts that consumer productivity will be greatest in springs characterized by a late onset and slow rate of increase in resource availability and lowest in springs with early onset and rapid increase in resource availability on summer ranges. As well, moderate levels of consumer productivity may be realized in early springs if the rate of increase in resource availability is slow, thereby allowing for at least partial compensation for timing mismatch via relatively prolonged resource access. Conversely, benefits of timing match in late springs may be reduced or lost entirely if resource availability increases rapidly, thereby also resulting in comparatively moderate levels of consumer productivity.

Results and Discussion

In accordance with previous analyses of shorter subsets of these data (27, 36), the annual timing of vegetation green-up at the study site advanced significantly over the period of observation but the timing of offspring production by caribou did not (Figure 2). As a result, the timing of resource demand by caribou during the critical period for offspring provisioning was generally coincident with the timing of resource availability in the early years of this study, but it increasingly lagged resource availability as the study progressed (Figure 2).

Mean spring temperature in the months immediately preceding and during vegetation green-up (April - May) was warmest in early rapid springs and coldest in late slow springs (Wald Chi-Square = 13.4, $P = 0.004$; supplemental Figure S2). Accordingly, the annual timing of vegetation green-up at the study site was approximately two weeks earlier in early rapid springs compared to late slow springs (Wald Chi-Square = 63.4, $P < 0.001$; Figure 3a). Likewise, the rate of vegetation green-up was approximately 25% more rapid in early rapid compared to early slow springs, and nearly twice as rapid in late rapid compared to late slow springs (Wald Chi-Square = 57.0, $P < 0.001$; Figure 3b).

The timing of resource demand defined as the timing of offspring production by caribou did not, however, differ across early rapid, early slow, late rapid, or late slow springs (Wald Chi-Square = 0.20, $P = 0.98$; Figure 4a). This suggests a lack of adjustment of the timing of offspring production by caribou in response to variation in the timing and rate of increase in availability of forage resources used for offspring provisioning. If so, any such lack of adjustment may have consequences for the magnitude of offspring production. Consistent with the predictions of our framework (Figure 1), offspring production by caribou was lowest in springs characterized by an early and rapid increase in availability of forage resources for provisioning offspring and greatest in springs characterized by a late and slow increase in availability of forage resources (Wald Chi-Square = 159.6, $P < 0.001$). In fact, offspring production was three-fold lower in early rapid springs compared to late slow springs (Figure 4b).

Our framework also suggests that long-distance migratory breeders may be able to compensate for mismatches in the timing of resource availability relative to timing of resource demand in early springs if resource availability also increases slowly (Figure 1). We found modest support for this prediction, with caribou offspring production slightly greater in early slow springs than in early rapid springs (Figure 4b). Conversely, the framework predicts that advantages for offspring production in late springs that promote phenological match between the timing of resource demand and resource availability might be constrained if resource availability also increases rapidly (Figure 1). There was comparatively strong support for this prediction, as caribou offspring production in late rapid springs was less than half that in late slow springs (Figure 4b).

Finally, the framework also suggests that interactions between timing and rate of increase in resource availability may have stronger positive or negative effects on offspring production than individual effects. This is indicated by darker purple or green shading in regions of overlap in the 2x2 matrix (Figure 1b) compared to the degree of shading in the binary panels above the matrix (Figure 1a). To assess this, we compared the strength of interaction- vs. individual terms in separate models of caribou offspring production. The Wald Chi-Square statistic reported above for the interaction between timing and rate of increase in resource availability (159.6) was nearly twice that for either individual term, both of which were also significant (timing = 99.3, $P < 0.001$; rate = 87.6, $P < 0.001$). Moreover, mean offspring production was approximately twice as great in late (0.44 ± 0.02) than in early springs (0.20 ± 0.01), and was also twice as great in slow (0.44 ± 0.02) compared to rapid springs (0.21 ± 0.02), while the difference between early rapid and late slow springs was three-fold (Figure 4b). Taken together, these results suggest that interactions between timing and rate of increase in resource availability had greater effects on offspring production than did singular effects of either variable.

Caribou, wild reindeer, and their domesticated counterpart, reindeer (all *Rangifer tarandus*), are critically important to the food security, cultural integrity, traditional knowledge transfer, economies, and resilience to environmental changes of Indigenous People and local communities throughout the far north (39-42). Abundance of caribou at the Kangerlussuaq study site has declined by nearly 75% in a little over a decade following a peak in 2006, and has remained comparatively low at the site since then (28). Globally, the abundance of *Rangifer* has declined by approximately 50% over the past 2-3 decades (43), with a loss of about thirteen percent of their global abundance between 2016 and 2021 alone (44). The decline in global *Rangifer* abundance has spurred a recent re-classification of the conservation status of this species complex from Least Concern to Vulnerable by the International Union for the Conservation of Nature (IUCN) (44). The IUCN's designation now renders *Rangifer* the only arctic ungulate whose conservation status is of greater priority than Least Concern on its Red List of Threatened Species (45). Though not clearly attributable to any single cause, the global decline of *Rangifer* has coincided with a period of rapid and accelerating arctic warming (43). Moreover, offspring production is an undeniably important component of population dynamics in any species, and in long-distance migratory breeders it may be particularly vulnerable to phenological mismatch related to climate change (13). Currently, all but two of 22 herds of migratory tundra *Rangifer* are in decline (25). In addition to their importance to traditional livelihoods, *Rangifer* can, through grazing, snow trampling, and fecal and urinary nitrogen inputs to soil, buffer tundra plant communities against warming-driven biodiversity loss (46-49). Hence, their conservation and management in the face of ongoing climate change will promote both biotic integrity and the maintenance of multi-faceted ecosystem services in this rapidly warming region. The extent to which recovery of declining *Rangifer* populations might be sensitive to phenological mismatches with advancing vegetation green-up on calving ranges as the Arctic continues to warm (*sensu* (23)) warrants more deliberate, and perhaps urgent, consideration. We suggest that a fruitful next step may include comparative assessments of conditions under which existing, developing, or future phenological mismatches may amplify more direct risks to imperiled *Rangifer* populations.

Materials and Methods

Testing predictions of the framework - study site and methods

We monitored the annual timing and magnitude of offspring production by caribou, and the annual timing and rate of green-up of plant species consumed by caribou, at a long-term study site adjacent to a core calving area located approximately 20km east of the village of Kangerlussuaq, Greenland. The study site lies within the UNESCO World Heritage site Aasivissuit-Nipisat that was designated as such in 2018. Monitoring of caribou calving and plant phenology at the site was conducted annually in 1993 and 2002 through 2022, with the exception of 2020 when travel restrictions were imposed due to the COVID-19 pandemic.

Caribou calving phenology and calf production - We used previously published data on caribou calving phenology (27) and calf production (28) complemented with more recent data collected using the same methodology, which is summarized here. Caribou were counted on a daily or near-daily basis each year from a series of promontories along a fixed route (28). Counts began in early to mid-May each year and progressed through June in order to encompass the entire period from pre-calving through early post-calving. Total numbers of calves, adult females, and non-classifiable adults were recorded on each day of observation. As described previously (27, 29), the timing of calving was derived from estimates of the daily proportion of calves observed among counts of calves and adult females. These counts revealed increasing proportions of calves as the calving season progressed each year, culminating in an annual maximum calf proportion, which was then assumed to represent 100% births for that year. Working backward from the count on that date each year, we used Caughley's Indirect Method A (30, 31) to retrospectively calculate the presumed percent births on each prior date of observation. To these data we then applied a non-linear model of the form:

$$Y = 1/(1 + e^{-(a+bX)}) \tag{1}$$

in which *Y* is percent births and *X* is day of year for a given year. This model was fit to each year of data, and the resulting estimates of coefficients *a* and *b* were used to calculate dates on which 50% of births (the mid-point of the calving season) occurred each year (27). In *Rangifer*, timing of calving is typically highly synchronized among females within a population (32-34). Consequently, daily counts of the number of calves per adult female during the annual calving season display sigmoidal behavior, with an abrupt onset of calving and rapid increase to a plateau followed by a slight decline as the calving season progresses through peak calf production and subsequent early calf mortality (32). Therefore, to derive an estimate of annual calf production that accounted for reductions due to neonatal calf mortality by the end of the calving season, we used the latest possible count of calves per adult female that included at least 20 adult females (27, 35, 36).

Plant phenology - As with the caribou calving data, we used previously published data on plant phenology from the same sources (27, 28) complemented with more recent data collected using the same methods, which are summarized here. We recorded phenophases of all plant species present on marked plots that were visited on a daily or near-daily basis during the same annual period during which caribou counts were conducted (27, 36). A species was considered to be in an emergent state of new annual growth and thus available as forage for caribou, if it displayed green leaf tissue (in the case of forbs), green basal meristematic tissue (in the case of grasses and sedges), or open leaf buds (in the case of deciduous shrubs). These data provided repeated counts of the number of species in an emergent state on each plot for each date of observation every year. The annual date on which the maximum number of species was recorded as emergent on each plot was considered the annual date of full (i.e., 100%) emergence or availability of caribou forage species for that year. Using the numbers of species recorded as emergent on each prior date of observation for each plot we then retrospectively calculated the percentage of the maximum number of species emergent on each plot on each date of observation for each year. These were then averaged across all plots in each year to derive annual estimates of the site-wide percent of species emergent and available as newly produced forage for caribou each year.

Estimation and analysis of annual timing and rate of increase in resource availability - We applied the model in equation (1) to annual data on the mean daily percentage of plant species present on our phenology plots and used the resulting estimates of coefficients *a* and *b* to calculate the annual dates of onset (5% of species emergent) and mid-point (50% of species emergent) of vegetation green-up at the site. To be consistent with previous analyses of a shorter subset of these data (27), we used the annual date of 50% species emergence as an index of the annual timing of resource availability for caribou during the calving season. Over the period encompassing this study (1993, 2002 - 2022), the mean day of year on which 50% of forage species had emerged was day 146.8 (approximately May 27). Years on which 50% emergence occurred earlier than this were considered “early” springs, while those on which 50% emergence occurred later were considered “late” springs (supplemental Figure S1a). The coefficient *b* from equation (1) provided a slope estimate quantifying the annual rate of vegetation green-up at the site. The annual rate of green-up was strongly positive related to the annual dates of 5% and 50% species emergence, but more closely related to the former (supplemental Figure S1b). We used the residuals of the non-linear model fit to the relationship in Figure S1b to categorize the annual rate of increase in resource availability for calving caribou as “rapid” (positive residuals) or “slow” (negative residuals; supplemental Figure S1b). These classifications resulted in an equitable distribution of the timing and rate of increase in resource availability among years, with 5 early rapid springs, 6 early slow springs, 5 late rapid springs, and 5 late slow springs.

Analyses of timing and rate of increase in resource availability and abiotic conditions in relation to early or late and rapid or slow springs - We used separate generalized linear models (GLMs) with an identity link function to analyze variation in timing and rate of increase in resource availability across categories of springs. The GLMs included either annual dates of 50% species emergence or estimates of *b* derived as detailed above as the dependent variable and spring categories “early” or “late” and “rapid” or “slow” as predictor variables. A continuous covariate, “year”, was included in both models to account for any potential trends in the dependent variables. Both models included an interaction term for early/late*rapid/slow and a separate term for year. To investigate variation in spring abiotic conditions across categories of springs, we used the same approach but with mean temperature for the months of April and May as the dependent variable because these are the months most immediately proximal to the onset of vegetation green-up at the site. Weather data were obtained from the Danish Meteorological Institute.

Analyses of caribou calf production in relation to timing and rate of increase in spring resource availability - We used a binomial generalized linear model (GLM) with a logit link function to analyze caribou calf production in relation to categorical spring resource conditions. This approach treats annual rates of offspring production as successful outcomes (number of calves) per trial (number of adult females), and thereby avoids challenges inherent to parametric analyses of ratio data (37, 38). The model included the annual count of caribou calves as the response variable; the annual number of adult female caribou associated with that number of calves as the trials variable; two nominal predictor variables categorizing spring resource availability as “early” or “late” and “rapid” or “slow”; and a numerical covariate for the day of year on which the final count of calves per adult female was obtained each year to account for any potential effect on estimates of calf production of variation among years in the timing of our counts.

Data availability

Original data will be made publicly available prior to publication on the Arctic Data Center repository.

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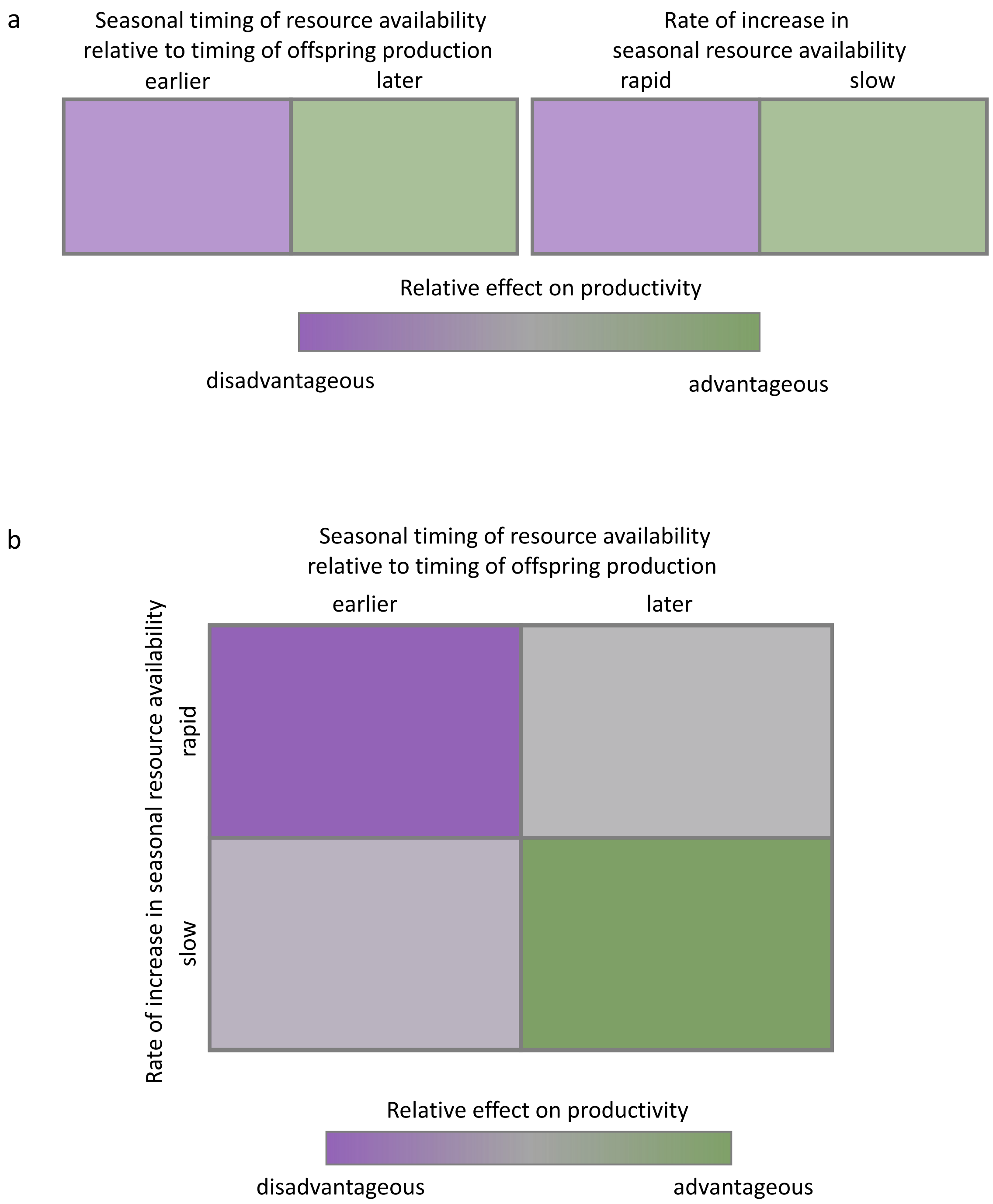

Figure 1. A framework for predicting relative effects on productivity of long-distance migratory breeders of the annual timing and rate of increase in availability of resources used for provisioning offspring on summer ranges where offspring are produced. In the upper panel (a), the timing of resource availability is categorized as early (light purple) or late (light green) relative to the timing of resource demand by consumers. Here, the timing of resource demand

by consumers refers to the critical period of offspring production and provisioning in seasonal breeders. Similarly, the rate of increase in seasonal resource availability can be categorized as rapid (a, light purple) or slow (a, light green). Building upon predictions of the phenological match-mismatch hypothesis, singular effects of earlier timing and a rapid rate of increase in resource availability are predicted to be disadvantageous for consumer productivity while later timing and a slower increase in resource availability are predicted to be relatively advantageous. When overlain, these singular effects are predicted to become interactive (b), either amplifying their individual effects (darker purple or green cells) or constraining/offsetting their individual effects (gray cells). Hence, disadvantages for consumer productivity of earlier availability of resources on summer ranges are predicted to be exacerbated by a rapid increase in resource availability (b, dark purple cell) but potentially mitigated by a slow increase in availability (b, lower gray cell). Similarly, advantages for consumer productivity of later availability of resources on summer ranges are predicted to be complemented by a slow increase in availability (b, dark green cell) but constrained or offset by a rapid increase in resource availability (b, upper gray cell).

Figure 2. The annual timing of resource demand (orange symbols) by a long-distance migratory breeder, tundra caribou, represented by the annual date of 50% births in the population; and the annual timing of resource availability (green symbols) for provisioning offspring, represented by the annual date of 50% vegetation green-up on the caribou calving range at a study site near Kangerlussuaq, Greenland over the period 1993 and 2002 - 2022. A linear model fit to annual estimates of the day of year on which 50% caribou births occurred (see Methods) was not significant (*b* = 0.087 ± 0.11, *P* = 0.43). A linear model fit to annual estimates of the day of year on which 50% of caribou forage species were emergent (see Methods) was significant (*b* = -0.73 ± 0.22, *P* = 0.004).

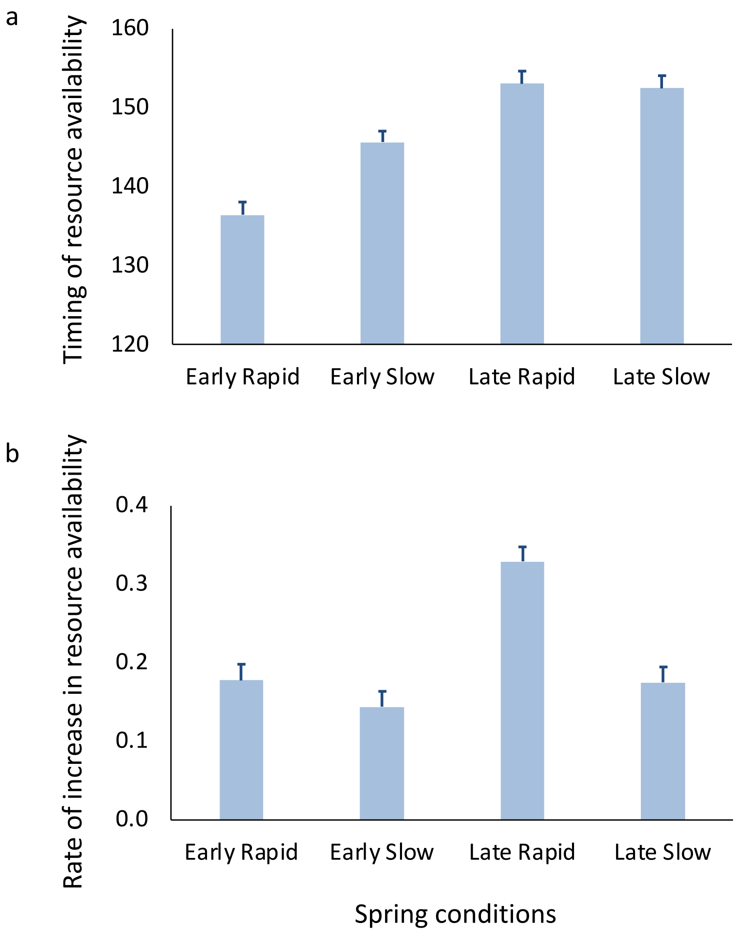

Figure 3. Variation across categories of spring conditions in (a) mean annual timing of availability and (b) mean annual rate of increase in availability of forage resources used by migratory tundra caribou to support costs of offspring production and provisioning on a calving range near Kangerlussuaq, Greenland for the period 1993, 2002 - 2022. Timing of resource availability is the annual date of 50% vegetation green-up, and rate of increase in resource availability is the annual rate of vegetation green-up, at the study site. Shown are estimated marginal means (± 1 SE) for each category derived from generalized linear models (see Methods).

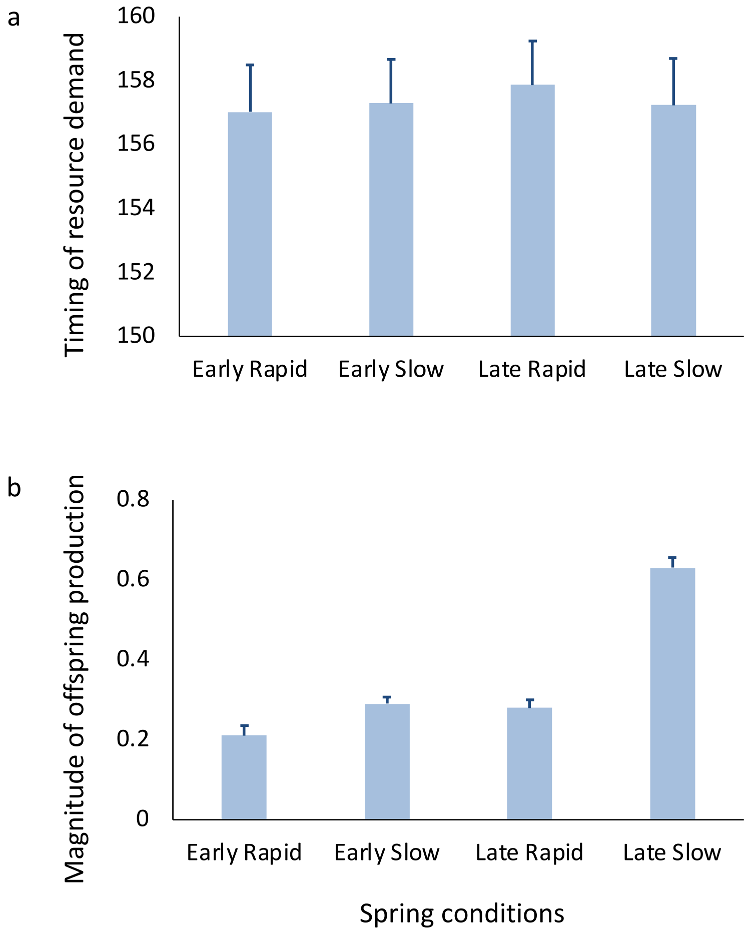

Figure 4. Variation across categories of spring conditions in (a) mean annual timing of resource demand by migratory tundra caribou defined as the day of year on which 50% of births were estimated to have occurred and (b) mean annual magnitude of offspring production defined as the ratio of calves per adult female caribou observed at the end of the calving season each year on a calving range near Kangerlussuaq, Greenland for the period 1993, 2002 - 2022. Shown are estimated marginal means (± 1 SE) for each category derived from generalized linear models (see Methods).

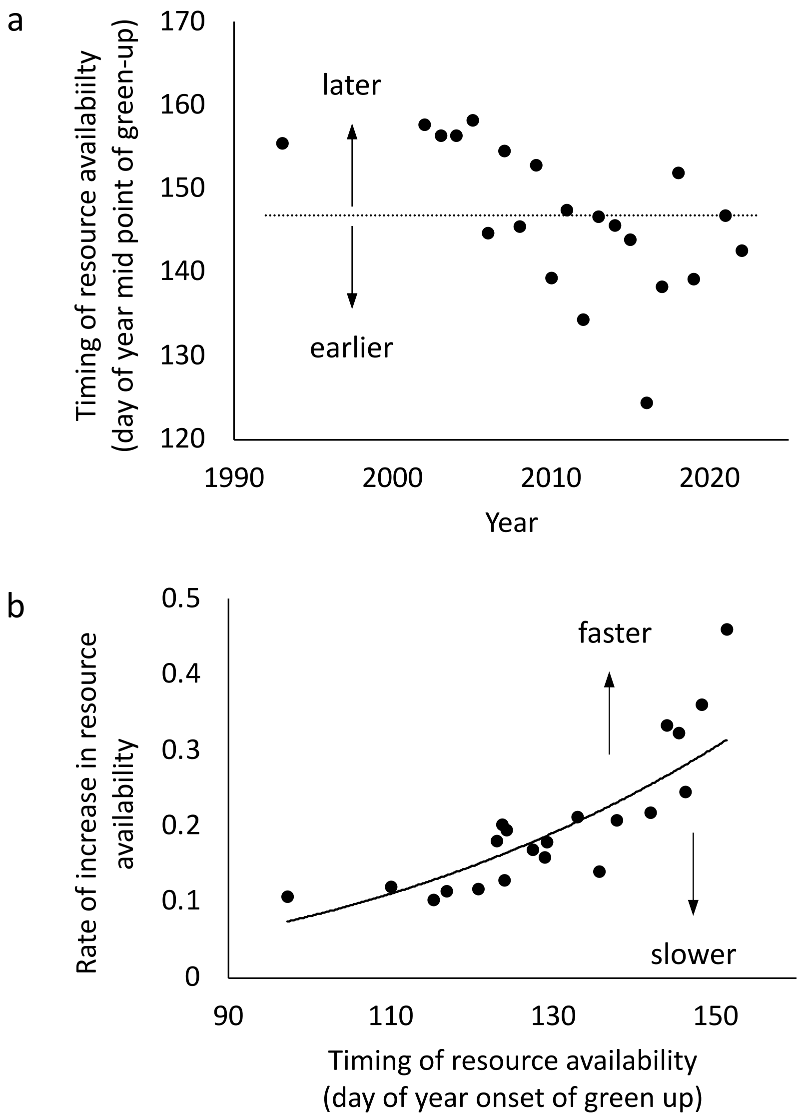

Fig. S1. Annual estimates of the timing of availability (a) and rate of increase in availability of resources (b) used by migratory tundra caribou to support the costs of offspring production and provisioning at the study site near Kangerlussuaq, Greenland, for the period 1993, 2002 - 2022. Timing of resource availability is the estimated annual day of year on which 50% of forage species were emergent. Rate of increase in resource availability is the estimate of coefficient *b* from equation (1) fit to annual estimates of the mean daily proportion of the final number of forage species present on plots monitored prior to and during the caribou calving season at the study site (see Methods for details). Categorization of spring conditions as “early” or “late” for the predictive framework shown in Figure 1 was based on negative or positive deviation, respectively, of annual values (dots) from the long-term mean (dashed line) in panel a. Categorization of spring conditions as “rapid” or “slow” was based on positive or negative deviation, respectively, from the non-linear model fit to the relationship between annual values of *b* and annual values of the day of year on which 5% of forage species were emergent at the site (solid line; $R^2 = 0.76$) in panel b. A similar model fit to the y-axis values in panel b using data on annual dates of emergence of 50% of forage species provided a poorer fit ($R^2 = 0.43$).

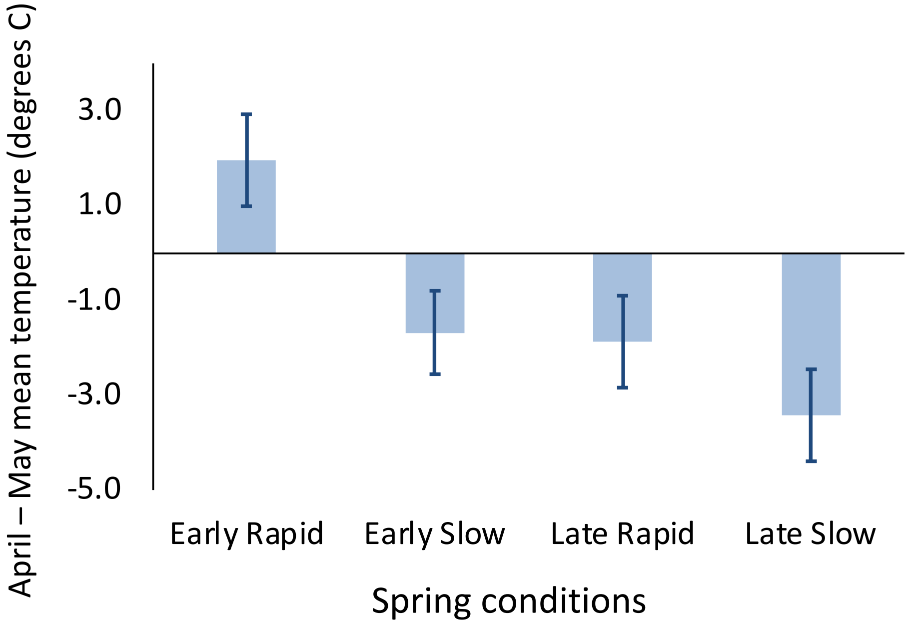

Fig. S2. Variation in mean temperature for the months of April and May across categories of spring conditions defined as described in the Methods section. Shown are estimated marginal means (± 1 SE) for each category derived from generalized linear models (see Methods).