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Autumn conditions as a driver of spring phenology in a free-living arctic mammal

Michael J Sheriff^{1*}, C Loren Buck² and Brian M Barnes³

Abstract

Background: Several studies have shown that birds and mammals are breeding earlier in response to earlier spring conditions. Delay in the onset of winter should also affect reproductive timing and may allow for breeding later instead of earlier in spring, if extended autumns lengthen the season that food is available to offspring. Using 4 years of fine-scale environmental and phenological data of annual timing of hibernation and reproduction in two free-living populations of arctic ground squirrels in Northern Alaska, we show that the onset of winter snow-cover may influence females' spring phenology *via* its interaction with the timing of hibernation of young-of-the-year (YoY).

Results: At the Atigun site, snowmelt occurs 26 days earlier and snow-cover occurs 14 days later than at the Toolik site. Previously, we found that Atigun females emerged and bred earlier than those at Toolik; however, here we show that this shift is not equivalent in magnitude to the earlier timing of spring conditions. At Atigun, females emerged and bred 13 days prior to snowmelt, while those at Toolik emerged and bred 34 days prior to snowmelt. We also found, importantly, that YoY entered hibernation after a set amount of time from birth regardless of site or environmental conditions. This resulted in Atigun YoY entering hibernation 24 (females) and 12 (males) days before snow-cover, but those at Toolik entering hibernation 0 (females) days before and 9 (males) days after snow-cover. This may allow females at Atigun to breed later (relative to snowmelt) in spring but select for early emergence and breeding of females at Toolik to allow sufficient time for offspring growth and preparation for hibernation.

Conclusions: These results indicate that autumn conditions may influence subsequent spring phenology and changes in spring conditions may be only one factor influencing phenological shifts associated with climate change. We suggest that in areas with harsh spring conditions, such as the Arctic, animals may not shift their phenology to match earlier, but still unfavorable spring conditions, but may delay their timing of spring breeding if climate change also delays the onset of snow-cover, allowing sufficient timing for offspring growth and preparation prior to winter.

Keywords: Climate change, Seasonal variability, Arctic, Arctic ground squirrel, Hibernation, Trophic mismatch

Background

In highly seasonal environments, precise timing of annual physiological and behavioral events, such as migration, hibernation, and breeding, is critical for survival and reproductive success. Although natural selection often favors early reproduction [1], females must balance the trade-off between breeding too early under poor environmental conditions that compromise adult survival and breeding too late and not allowing sufficient time for offspring to grow and prepare for winter. Many studies are now showing that rapid changes in climate, and

concurrent shifts in seasonality, are creating a mismatch between timing of parturition and the availability of food, which can decrease reproductive success [2-6]. For example, in some European populations of the pied flycatcher (*Ficedula hypoleuca*), a mismatch between linked trophic levels has resulted in a decline in reproduction and recruitment, ultimately leading to a population decline [2]. Yellow-bellied marmots (*Marmota flaviventris*) in the Rocky Mountains of North America have also advanced their timing of emergence from hibernation and weaning of young, but in contrast to pied flycatchers, this has resulted in greater body mass of marmots prior to hibernation, decreased adult mortality, and an increase in population size [7]. Interestingly, although there has been a trend for warmer spring temperatures

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in the Rocky Mountains, the average date of snowmelt and thus the beginning of the growing season has not changed [8].

Understanding the organism and environment interactions known to influence the timing of reproduction has taken on a new urgency as climate change is altering environmental conditions during reproduction. Although several studies suggest that species are not responding optimally to environmental changes (e.g., [3-5,9-11]), many of these have investigated environment-reproduction mismatches in timing within avian species, which often rely on synchronizing reproduction to a single, seasonal peak in food availability for reproductive success (e.g., [2,12,13]). This mismatch hypothesis, however, may be less relevant in more generalist foraging species, and the relative importance of synchronizing reproduction with peaks in food availability may be more relaxed [14]. Further, most studies focus on climate-induced changes in spring and have not regarded the impact of changing autumn conditions on the timing of spring reproduction. Prolonged autumn conditions and a delay in winter snow-cover may allow offspring more time to prepare for winter and relax the urgency of early breeding and any cost to female condition in early spring.

In this study, we used free-living female arctic ground squirrels (AGS; *Urocitellus parryii*) to investigate how autumn conditions influence the timing of spring reproduction. AGS are a generalist herbivore, consuming roots, twigs, leaves, seeds and berries, and even some carrion. Food availability is limited by snow-cover because it prevents access; thus, the timing of spring snowmelt and winter snow-cover is critical for AGS. AGS are the most northern hibernator with a geographical range that reaches the shores of the Arctic Ocean [15]. In spring, males end torpor and return to continuously high body temperatures (required for gametogenesis [16]) 15–25 days prior to emergence from hibernation [17]; females come to high body temperature and emerge within 1–2 days, approximately 2 weeks after males, and mating occurs within 2–4 days [18-20]. In autumn, females enter hibernation first, 30–40 days before males [18-20]. Previously, we have shown that in areas where snowmelt occurs earlier, phenological events of AGS occur earlier in the calendar year [21]. However, the timing of spring snowmelt may not be the proximate driver of spring timing. In male AGS, we have shown that the return to high body temperature in spring corresponds to when males enter hibernation in autumn and that their emergence from hibernation and surface activity are timed to precede female emergence by 12 days [20]. Here, we investigated the timing of female AGS emergence in relation to the timing of spring snowmelt rather than calendar date, and how the previous onset of winter snow-cover may influence subsequent phenological events.

We compared four years of female and offspring phenological data from AGS inhabiting two nearby sites at similar latitudes, Atigun and Toolik in the Alaskan Arctic, which experience different snow-cover regimes. At Atigun, less snow falls and spring snowmelt occurs on average 26 days earlier and snow-cover occurs on average 14 days later than at Toolik [20]. In the context of these differences in snow-cover, we precisely measured the following: 1) the timing of adult female emergence from hibernation and parturition in relation to the timing of spring snowmelt (AGS emerge prior to snowmelt); 2) the timing of adult female entrance into hibernation in relation to the timing of winter snow-cover; 3) the relationship between the timing of entrance into hibernation and emergence (emergence is significantly correlated to parturition in AGS [22]); 4) the average duration (days) that young-of-the-year (YoY) remained active (calculated as the length of time from birth date to entrance into hibernation); and 5) the timing of YoY entrance into hibernation in relation to the timing of winter snow-cover. We predicted that, because winter snow-cover is delayed at Atigun, YoY (and females) will have more time to prepare for winter, which could allow females to emerge from hibernation later relative to snowmelt. At Toolik, the earlier onset of snow-cover will have forced females to emerge earlier relative to snowmelt to allow sufficient time for YoY to prepare for hibernation.

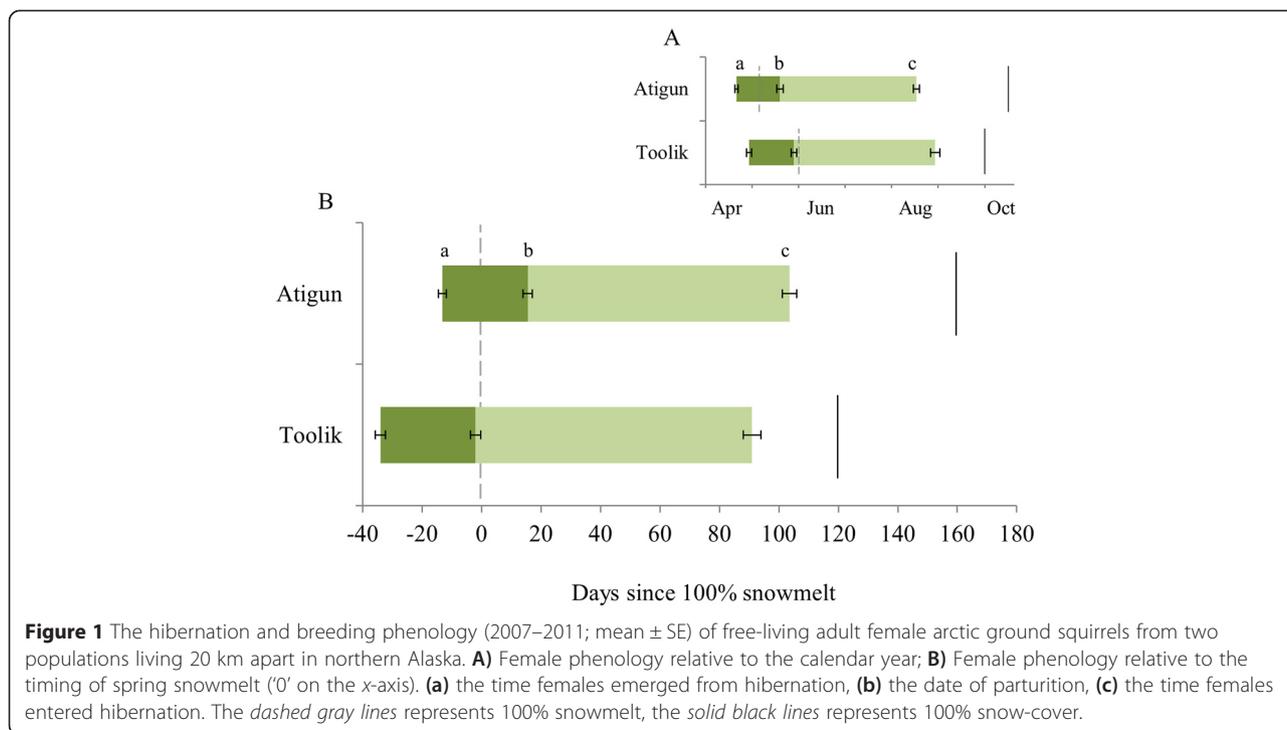
Results

Phenology of adult females

Adult females at Atigun both emerged from hibernation and gave birth significantly closer to the timing of snowmelt in spring compared to females at Toolik (emergence: $Z = -5.73$, $P < 0.0001$; parturition: $F_{1, 18} = 92.83$, $P < 0.0001$). This comparison was consistent over the four years of observations (no year effect on emergence: $Z = 0.68$, $P = 0.49$, or parturition: $F_{1, 18} = 0.22$, $P = 0.80$). Atigun females emerged 13 ± 1 days prior to snowmelt and gave birth 16 ± 2 days after snowmelt, while Toolik squirrels emerged 34 ± 2 days prior to snowmelt and gave birth 2 ± 2 days prior to snowmelt (Figure 1).

In relation to the timing of snow-cover and onset of winter conditions, adult females at Atigun entered hibernation significantly earlier than females at Toolik ($Z = 5.07$, $P < 0.0001$). We found no year effect ($Z = 1.49$, $P = 0.14$). Atigun females entered hibernation 59 ± 2 days prior to snow-cover, while Toolik squirrels entered 30 ± 3 days prior to snow-cover (Figure 1).

Overall, we found a significant relationship between the date when females entered hibernation and the date when they emerged ($r^2 = 0.40$, $F_{1, 44} = 16.58$, $P < 0.0001$). However, this was driven by differences between the sites ($F_{1, 44} = 22.29$, $P < 0.0001$); within a site the time at which females emerged from hibernation was not related



to when they entered ($F_{1, 44} = 1.11, P = 0.30$). Thus, we conclude that the date that individual females enter hibernation is not predictive of when they emerge in spring.

Phenology of young-of-the-year

Female YoY remained active above ground for a significantly shorter duration than male YoY ($F_{1, 23} = 27.64, P < 0.0001$), but, importantly, we found no difference in the length of the active season between the sites ($F_{1, 23} = 0.94, P = 0.34$; Tukey HSD post-hoc male $P = 0.82$, female $P = 0.96$). In relation to the timing of the onset of snow-cover, YoY at Atigun entered hibernation significantly earlier than those at Toolik ($F_{1, 23} = 29.18, P < 0.0001$), and females entered hibernation significantly earlier than males ($F_{1, 23} = 6.60, P = 0.02$). Female YoY required 116 ± 2 days at Atigun and 114 ± 2 days at Toolik from birth to entrance into hibernation, but those at Atigun entered hibernation 24 ± 3 days before snow-cover, while at Toolik female YoY entered hibernation 0 ± 3 days before snow-cover (Figure 2). Male YoY required for 134 ± 5 days at Atigun and 130 ± 4 days at Toolik, but those at Atigun entered hibernation 12 ± 7 days before snow-cover, while at Toolik male YoY entered hibernation 9 ± 3 days after snow-cover (Figure 2).

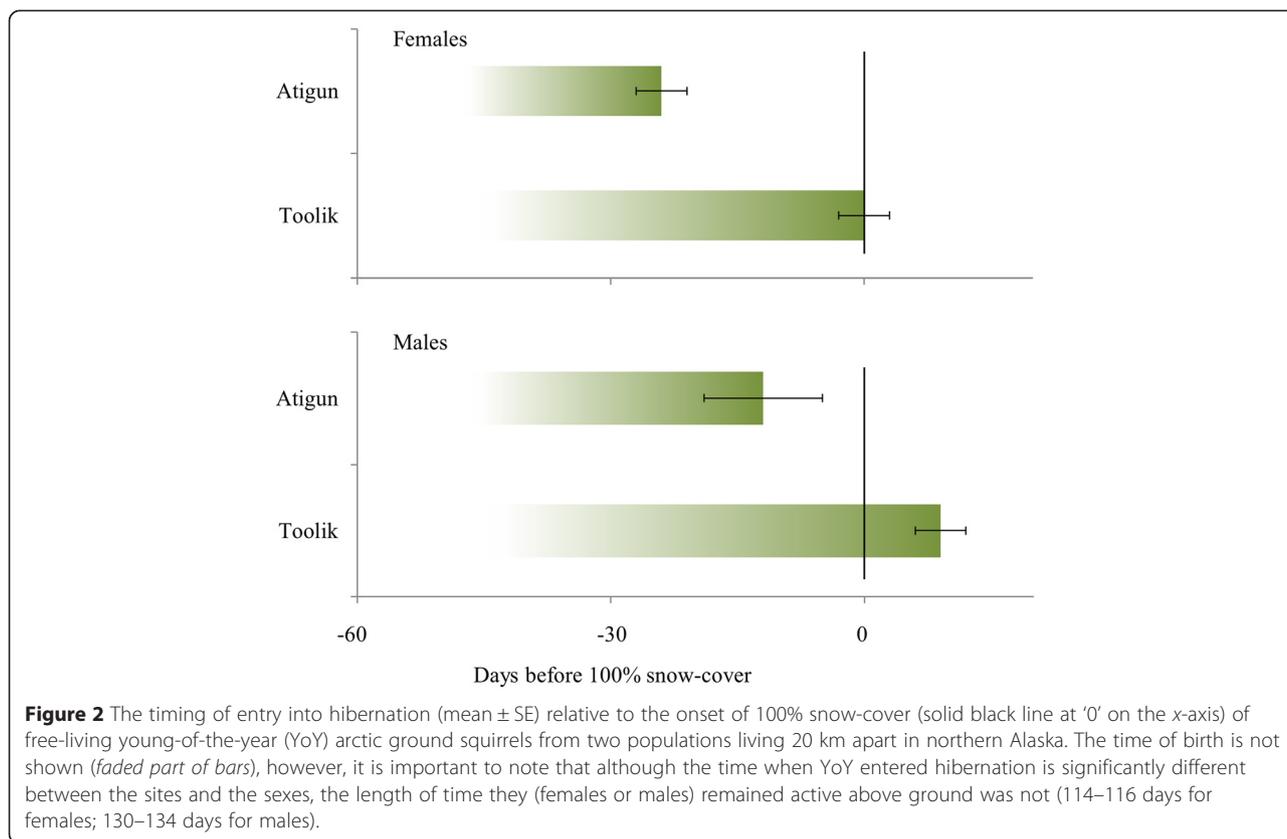
Discussion

Breeding phenology

In highly seasonal environments, an important evolutionary factor that shapes the decision of when to breed

is the seasonal variation in food availability. Selection will favor those animals that breed when adequate food is available, and the earliest breeders often have the greatest fitness [1]. A key factor in this decision making is to maximize the time offspring have to grow and prepare for winter; however, this selection is opposed by constraints and costs to the parents of breeding too early [23]). Although climate warming has led to shifts in breeding phenology of many species, a growing body of evidence shows that more generalist animals or those living in environments with relatively constant or abundant food throughout the breeding season may become mismatched with food availability, but this mismatch may not have the often assumed consequences of a reduction in reproductive success (e.g., [7,14,24]). Our results suggest that another factor influencing the timing of and success of spring reproduction may be changes in autumn conditions.

Prolonged snow-free conditions or delays in onset of winter snow-cover could allow adult females to delay breeding in spring while still providing sufficient time for young to grow and prepare for winter. This may be especially important for animals that breed in areas where harsh spring conditions—low temperatures and poor food availability, characteristic of the Arctic—coupled with reproduction, require high energy output with little chance for intake. Like many other animals, female AGS are advanced in their timing of breeding at Atigun where snowmelt occurs earlier as compared to Toolik [21]. However, the observed earlier breeding is not equivalent to the



advanced onset of snow-free conditions; snow-free conditions occur 26 days earlier at Atigun compared with Toolik, but females breed only 13 days earlier. Essentially, Atigun females have delayed their breeding with respect to spring conditions, emerging and breeding in a more favorable environment compared to Toolik females (Figure 1). Their young still have sufficient time to grow and fatten in preparation for hibernation, however, and do not experience a shorter active season because at Atigun winter snow-cover occurs 14 days later than at Toolik. We found that Atigun YoY enter hibernation 24 (females) and 12 (males) days before snow-cover while Toolik YoY enter hibernation 0 (females) days before and 9 (males) days after complete snow-cover (Figure 2). Critical in this is that YoY remain active for similar durations at both sites, suggesting that there is an endogenous temporal program that governs the timing of entrance into hibernation of YoY and that animals are not simply responsive to environment with respect to immergence; i.e., Atigun YoY do not take additional advantage of longer snow-free time, while Toolik YoY (especially the males) do not truncate their activity due to the earlier onset of winter snow-cover. Remaining on the surface may be more risky in terms of predation than beginning hibernation once prepared and thus, may be selected against. Indeed, captive studies of ground squirrels clearly indicate that timing and

expression of hibernation, reproduction, and growth are under endogenous control and persist for a year in the absence of environmental cues that can be entrained by photoperiod [25]. Thus, at Atigun, the prolonged snow-free period allows adult females the ability to relax the timing of spring breeding while still allowing maximum time for their offspring to grow and prepare for winter. However, at Toolik, the constraints of early winter snow-cover force females to emerge to a near 100% snow-covered environment in spring to allow sufficient time for their offspring to grow and fatten in preparation for winter. These results suggest that seasonal variation in autumn may be important to consider to fully understand phenological shifts made in spring.

Ecologists are challenged with predicting how organisms and populations will respond to climate-induced changes to local and global ecosystems. Although we have begun to understand some of the responses of free-living animals to changing seasonality, the physiological mechanisms which drive climate-induced organismal responses are often underappreciated. For example, in animals, glucocorticoids play a critical role allowing animals to cope with and respond to extreme changes in their environment [26,27]. These hormones are important for shaping the behavior and morphology of individuals, can alter population and community dynamics *via* their effects on survival and reproduction, and can have

generational effects shaping the phenotype of offspring [28–32]. Yet our understanding of the role glucocorticoids may play in response to changing seasonality is limited (but see [33]). Further, physiological mechanisms may limit the ability of organisms to respond. For example, the relationship between phenology and environmental variability is recognized as a key concern; however, largely overlooked is the extent to which phenological adjustments are regulated by biological time-keeping mechanism and circannual clocks, and the degree of flexibility built into these clockworks [25,34]. This may be of particular importance in hibernating mammals, where studies have shown the critical role of a relatively rigid, endogenous circannual clock in the persistence and timing of annually recurring seasonal events [25,35]. In AGS this may limit their ability to respond to a changing environment, particularly adult males [20]. An understanding of the mechanisms of and limitations to organisms' physiological capacities will improve our ability to predict when and where organisms can cope with change and where change may be too extreme.

Conclusions

Although there is widespread evidence of shifts in breeding phenology of animals in response to climate change [5,6], there is great concern that the magnitude of change, *via* physiological plasticity or microevolution, will not be sufficient to keep pace with the rapid climate-induced changes in food availability [2,9,36]. In many species, mismatches between breeding and food availability have led to a decline in reproductive success [3,4,9,11,37,38]. Previously we have also shown that in areas with earlier spring snowmelt AGS emerge from hibernation and breed earlier [21]; however, as we demonstrate here, the response by AGS is not equivalent to the environmental difference, *i.e.*, spring conditions have advanced more than AGS phenology (Figure 1). In an area where snowmelt occurs earlier in the calendar year, females delay their breeding relative to snowmelt (Figure 1), and our results suggest this timing may be influenced by prolonged autumn conditions, which allow longer time for offspring to grow and prepare for winter hibernation (Figure 2). Conversely, in an area where snowmelt occurs later in the calendar year, females bred early relative to snowmelt (Figure 1) possibly driven by an early onset of winter snow-cover and less time available for their offspring to grow and prepare for winter (Figure 2).

Methods

Study area and estimates of snow-cover

This study occurred at two sites, separated by about 20 km along the Dalton Highway in Northern Alaska: Toolik Lake (68° 38' N, 149° 38' W; elevation 719 m)

and Atigun River (68° 27' N, 149° 21' W; elevation 812 m). The topography is relatively flat, with gently rolling hills underlain by continuous permafrost with a depth of thaw of 1–2 m [39]. Entrances to AGS burrows between sites did not differ in exposure to or shelter from solar radiation, shade, or wind. Although the plant community in areas occupied by AGS may differ between the sites, we do not believe this to have an effect on AGS phenology due to the fact that AGS are such a generalist herbivore.

Snow-cover was quantified from 2007 to 2011 using a camera (Campbell Scientific, CC640 Digital Camera System mounted inside a Pelco EH4700 Environmental Enclosure) mounted on a tower facing across each of the study areas that acquired a daily image at solar noon. To describe snow cover differences among years and between our two sites, we recorded the day each site was first 100% snow-free and remained so for ≥ 3 days in spring and the day each the site became 100% snow-covered for ≥ 3 days in autumn. Spring snowmelt occurs on average 26 days earlier at Atigun than at Toolik, and in autumn snow-cover occurs on average 14 days later at Atigun than at Toolik. Thus, Atigun has a 40 day longer snow-free season than Toolik, which potentially extends the foraging season there for AGS.

Estimates of phenology

Phenological data was recorded from autumn 2007 until autumn 2011 for adult females ($n = 29$ and 22 at Atigun and Toolik, respectively) and from autumn 2007 until autumn 2010 for juveniles ($n = 15$ and 12 at Atigun and Toolik, respectively). Squirrels were captured using Tomahawk live traps baited with carrot set in the early morning and checked every 1–3 h until closure in the mid-afternoon. Captured animals were transported to the Toolik Field Station of the University of Alaska Fairbanks. Animals were anesthetized by a 3–5 min exposure to isoflurane vapors and uniquely tagged (ear tags—Monel #1; pit tags—AVID MUSICC). Animals were then abdominally implanted, and subsequently explanted 6–12 months later, with temperature-sensitive data loggers (modified TidBit Stowaway model TBICU32-05 + 44, Onset Computer Corporation; or iButtons, Maxim Integrated) that were programmed to record core T_b at 20 min or 120 min intervals (see [40] for surgical details). After surgery, animals were monitored for 12 h prior to release at their site of capture. Patterns of T_b change recorded by the loggers give the precise timing of hibernation and parturition in AGS (see [41] for validation). Procedures were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee, and field work was conducted under state and federal permits.

Statistics

To test for differences in phenology between the sites, we used analysis of variances (ANOVAs) (year x site) or Mann–Whitney U tests for non-parametric data. The relationship between entrance into hibernation and emergence was evaluated using a general linear model. The length of YoY activity was calculated as the length of time from the average birth date of a given year until an individual entered hibernation and compared using ANOVAs (sex x site). The assumption of normality was tested with Shapiro-Wilks test, and the assumption of homogeneity of variances was tested with Levene's test. All statistics were performed using the software package STATISTICA 10. All data are expressed as means \pm 1 SE, unless otherwise stated.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MJS conceived of the study and drafted the manuscript with help from CLB and BMB. All authors collected the data, MJS analyzed the data. All authors read and approved the final manuscript.

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References

- Van Noordwijk AJ, McCleery RH, Perrins CM. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J Anim Ecol.* 1995;64:451–8.
- Both C, Bouwhuis S, Lessells CM, Visser ME. Climate change and population declines in a long-distance migratory bird. *Nature.* 2006;441:81–3.
- Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J Anim Ecol.* 2009;78:73–83.
- Both C, van Turnhout CAM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc R Soc B.* 2010;277:1259–66.
- Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature.* 2003;421:37–42.
- Root TL, Price JL, Hall KR, Schneider SH, Rosenzweig C, Pounds AJ. Fingerprints of global warming on wild animals and plants. *Nature.* 2003;421:57–60.
- Ozgul A, Childs DZ, Oli MK, Armitage KB, Blumstein DT, Olson LE, et al. Coupled dynamics of body mass and population growth in response to environmental change. *Nature.* 2010;466:482–5.
- Inouye DW, Barr B, Armitage KB, Inouye BD. Climate change is affecting altitudinal migrants and hibernating species. *Proc Natl Acad Sci U S A.* 2000;97:1630–3.
- Møller AP, Rubolini D, Lehikoinen E. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc Natl Acad Sci U S A.* 2008;105:16195–200.
- Post E, Forchhammer MD, Bret-Harte S, Callaghan TV, Christensen TR, Elberling B, et al. Ecological dynamics across the Arctic associated with recent climate change. *Science.* 2009;325:1355–8.
- Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, et al. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc R Soc B.* 2011;278:835–42.
- Reed TE, Jenouvrier S, Visser ME. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *J Anim Ecol.* 2013;82:131–44.
- Visser ME, van Noordwijk A, Tinbergen JM, Lessells CM. Warmer spring lead to mistimed reproduction in great tits (*Parus major*). *Proc R Soc B.* 1998;265:1867–70.
- Dunn PO, Winkler DW, Whittingham LA, Hannon SJ, Robertson RJ. A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore. *Ecology.* 2011;92:450–61.
- MacDonald SO, Cook JA. Recent mammals of Alaska. Fairbanks: University of Alaska Press; 2009.
- Barnes BM, Kretzmann M, Licht P, Zucker I. Influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. *Biol Reprod.* 1986;35:1289–97.
- Barnes BM. Relationships between hibernation and reproduction in male ground squirrels. In: Geiser F, Hulbert J, Nicol SC, editors. Adaptations to the cold: Tenth International Hibernation Symposium. Armidale, Australia: University of New England Press; 1996. p. 71–80.
- Buck CL, Barnes BM. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. *J Mammal.* 1999;80:430–42.
- Buck CL, Breton A, Kohl F, Tøien O, Barnes BM. Overwinter body temperature patterns in free-living arctic squirrels (*Spermophilus paryii*). In: Lovegrove BG, McKchnie A, editors. Hypometabolism in animals: torpor hibernation and cryobiology. Pietermaritzburg: University of KwaZulu-Natal; 2008. p. 317–26.
- Sheriff MJ, Richter MM, Buck CL, Barnes BM. Changing seasonality and phenological responses of free-living male arctic ground squirrels: the importance of sex. *Phil Trans R Soc B.* 2013;368:20120480.
- Sheriff MJ, Kenagy GJ, Richter M, Lee T, Tøien Ø, Kohl F, et al. Phenological variation in annual timing of hibernation and breeding in nearby population of arctic ground squirrels. *Proc R Soc B.* 2011;278:2369–75.
- Williams CT, Sheriff MJ, Kohl F, Barnes BM, Buck CL. Interrelationships among timing of hibernation, reproduction, and warming soil in free-living female arctic ground squirrels. In: Thomas R, Claudia B, Walter A, Eva M, editors. Living in a seasonal world. Berlin: Springer; 2012. p. 63–72. doi:10.1007/978-3-642-28678-0_6.
- Stevenson IR, Bryant DM. Climate change and constraints on breeding. *Nature.* 2000;406:366–7.
- Burger C, Belskii E, Eeva T, Laaksonen T, Mägi M, Mänd R, et al. Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. *J Anim Ecol.* 2012. doi:10.1111/j.1365-2656.2012.01968.x
- Williams CT, Barnes BM, Kenagy GJ, Buck CL. Phenology of hibernation and reproduction in ground squirrels: integration of environmental cues with endogenous programming. *J Zool.* 2014;292:112–24.
- Sapolsky RM, Romero LM, Munck AU. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr Rev.* 2000;21:55–89.
- Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, et al. Ecological bases of hormone-behavior interactions: the 'emergency life history stage'. *Amer Zool.* 1998;38:191–206.
- Buck CL, O'Reilly KM, Kildaw SD. Interannual variability of black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *Gen Comp Endocrinol.* 2007;150:430–6.
- Clinchy M, Sheriff MJ, Zanette LY. Predator-induced stress and the ecology of fear. *Funct Ecol.* 2013;27:56–65.
- Meylan S, Miles DB, Clobert J. Hormonally mediated maternal effects, individual strategy and global change. *Phil Trans R Soc B.* 2012;367:1647–64.
- Sheriff MJ, Love OP. Determining the adaptive potential of maternal stress. *Ecol Lett.* 2013;16:271–80.
- Love OP, McGowan P, Sheriff MJ. Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in

- individuals, with implications for populations and communities. *Funct Ecol.* 2013;27:81–92.
33. Wingfield JC, Owen-Ashley N, Benowitz-Fredericks M, Lynn SE, Hahn TP, Wada H, et al. Arctic spring: the arrival biology of migrant birds. *Acta Zool Sinica.* 2004;50:948–60.
 34. Helm B, Ben-Shlomo R, Sheriff MJ, Hut RA, Foster R, Barnes BM, et al. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proc R Soc B.* 2013;280:20130016.
 35. Pengelley ET, Aloia RC, Barnes BM. Circannual rhythmicity in the hibernating ground squirrel *Citellus lateralis* under constant light and hyperthermic ambient temperature. *Comp Biochem Physiol.* 1978;61:598–603.
 36. Visser ME, Both C. Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc B.* 2005;272:2561–9.
 37. Boggs CL, Inouye DW. A single climate driver has direct and indirect effects on insect population dynamics. *Ecol Lett.* 2012. doi:10.1111/j.1461-0248.2012.01766.x
 38. Post E, Forchhammer MC. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Phil Trans R Soc B.* 2008;363:2369–75.
 39. Buck CL, Barnes BM. Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. *J Mammal.* 1999;80:1264–76.
 40. Long RA, Hut RA, Barnes BM. Simultaneous collection of body temperature and activity data in burrowing mammals: a new technique. *J Wildl Manag.* 2007;71:1375–9.
 41. Williams CT, Sheriff MJ, Schmutz JA, Kohl F, Tøien Ø, Buck CL, et al. Data logging of body temperatures provides precise information on phenology of reproductive events in a free-living arctic hibernator. *J Comp Physiol B.* 2011;181:1101–9.

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