

# Environmental variability and phenology evolution: impacts of climate change and spring onset on reproductive timing in a small mammal

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## Abstract

The phenology, or timing of life history events, of organisms affects both ecological and evolutionary dynamics. Recent work has illustrated the effects of climate change on the phenology for many species. Changing selective pressures on phenology can have consequences for species if the reliability of phenological cues decreases or if climate change affects interacting species differentially. There are now numerous examples, in which earlier mean timing of spring has selected for earlier phenology of organisms. However, much less is known about how changes in the variability of spring—and consequently the reliability of cues—might affect species. We built a general model of animal population dynamics to study both the ecology and evolution of phenological events under climate change. We parameterized this model for a population of the collared pika (*Ochotona collaris*) found in the Yukon, Canada. In line with past work, we show that an earlier timing of spring snowmelt will select for an earlier timing of reproduction. In addition, we show that variability in the onset of spring also selects for earlier reproduction. However, evolution or plasticity in juvenile mortality, due to late snowmelt, can lead to later reproduction. These results highlight the importance of looking at the variability, and not only the mean, in spring onset. The specific relationship between the mean and variability of spring onset coupled with the ability of a population to be plastic or adaptable will determine the long-term effects of climate change on the phenology of species.

Keywords: adaptive dynamics, climate change, game theory, *Ochotona*, phenology, pika

## 1 Introduction

For many species their seasonal timing of life history events, or phenology, is important for both ecological and evolutionary dynamics (Forrest and Miller-Rushing 2010). Phenology includes the timing of migration, feeding, hibernation, mating, and reproduction. The specific timing of these events is important as each presents fitness and performance consequences (Forrest and Miller-Rushing 2010). For example, reproductive timing is often restricted to certain parts of the year and depends on factors like snowfall, food availability, and predation pressures (Bronson 2009, Boutin and Lane 2014). Often these factors have conflicting selective pressures on reproductive timing.

Climate change is already causing spring to occur earlier in many parts of the world (ACIA 2005). Changing selective pressures may lead to changes in phenology through phenotypic plasticity or evolutionary change (Merilä and Hendry 2014, Boutin and Lane 2014). The key question becomes will climate change outpace plastic and evolutionary responses? If climate change causes too rapid environmental change, then organisms may experience higher mortality or lower reproductive success. This can occur because of mismatches between the species of interest and other abiotic or biotic factors. With changing selective pressures for interacting species, this can lead to community level consequences (Visser 2008).

In addition to altering the mean timing of spring onset, climate change is expected to alter the variability in timing of spring onset (ACIA 2005). It is already well known that variability in seasonal factors can lead to population declines (Roland and Matter 2013). However, less is known about the how climatic variability affects evolution. This leads to the question of how phenological timing should evolve given a variable environment (Iwasa and Haccou 1994, Lof et al. 2012). Given a variable environment, bet hedging or other strategies may be favored (Childs et al. 2010). Evolutionary bet hedging refers to situations, in which it may be advantageous for an organism to reduce their current reproductive output in order to increase their overall fitness (Childs et al. 2010). Given harsh environmental conditions, it may be better to reduce reproductive capacity (or that of your offspring) and wait until better environmental conditions are present. For example, Lof et al. (2012) studied an optimality model of reproductive timing for great tits (*Parus major*). They found that mismatched timing of reproduction with respect to peak food abundance can be adaptive in settings where temporal variability is present. Follow up work found that great tit populations could only be rescued through plasticity and micro-evolution under mild climate scenarios (Gienapp et al. 2013). This leads to two general questions. First, how might phenology evolve under increasing variability due to climate change? And, second, how might predictions change between previously used optimality models and more realistic eco-evolutionary models?

Both environmental variability and climate change are expected to be particularly relevant at higher latitudes. At high latitudes seasonal selective pressures are particularly strong with large variability within and between years (Stevenson et al. 2015). In addition, climate change is predicted to affect the arctic region more than other parts of the world (ACIA 2005). To construct population models and to predict the effects of climate change, high-quality data must be available. One case study that fulfills both of these criteria is the group of animals known as pikas (family Ochotonidae). In recent years, concerns have developed about the effect of climate change on pikas (Wilkening et al. 2011, Beever et al. 2011, but see Smith and Nagy 2015, White and Smith 2018). The reasoning is that since pikas are cold-adapted, and typically live at higher elevations, they would be more susceptible to changes in temperature compared to other small mammals (Smith 1974b, Wilkening et al. 2011). The collared pika was recently listed as a species of concern by Canada, because of the potential effect of climate change on their populations in the near future (COSEWIC 2011). In the collared pika's range, climate change is predicted to induce an earlier onset of spring and the onset of spring will be more variable on a year-to-year basis (ACIA 2005). This earlier and more variable spring timing may make cues that pikas use more reliable or cause phenological mismatches between pikas and their food sources (COSEWIC 2011). Additionally, earlier spring timing may expose pikas to freezing rain events if snow cover is

not available (Smith 1978).

We have three primary aims: 1) to build a general model of phenology evolution that accounts for eco-evolutionary dynamics and environmental factors, 2) to investigate the role of environmental variability in driving evolutionary dynamics, and lastly 3) to explore how the variability, in addition to the mean, of spring affects evolutionary dynamics under projections of climate change. To account for realistic ecological dynamics and environmental factors, evolutionary game theory is appropriate. Evolutionary game theory, and more specifically adaptive dynamics, has already been used to study the evolution of phenology (Parvinen et al. 2006, Johansson and Jonzén 2012). Our general modeling framework incorporates physiology, population dynamics, and environmental factors to examine the evolution of reproductive timing. As a case study, we apply our model to a population of collared pika found in Ruby Ridge, Yukon, Canada (Franken and Hik 2004a, COSEWIC 2011). This population is a particularly good study system because of a long-term census and previously collected life-history data.

## 2 Model and methods

We are interested in organisms that have a specific window of the year in which they can reproduce, the reproductive season. A reasonable framework for this type of system is a semi-discrete, or hybrid, model (Mailleret and Lemesle 2009, White and Hastings 2018). More specifically, we model within-reproductive season dynamics as a continuous process (hereafter termed within-season dynamics) and discrete model from one year to the next (hereafter termed between-season dynamics). Within-season dynamics are modeled with a set of ordinary differential equations that track population density for two life stages (juveniles and adults), their respective resource reserves, resource density, and the environment. Environmental conditions are tracked during the season and can affect survival or reproduction. The semi-discrete model also allows for stochasticity in the timing of within-year dynamics (i.e. the timing of spring).

We model both adult population density ( $A(t)$ ) and juvenile population density ( $J(t, \tau)$ ) through time,  $t$ .  $J(t, \tau)$  is the density of juveniles born at time  $\tau$  that are alive at time  $t$ . Juveniles born at different times will have different lengths of time to collect resources before winter and will be more or less affected by late season snowfall. Both adults and juveniles have haypile sizes that change over the course of the season, denoted adult haypile size ( $B_A(t)$ ) and juvenile haypile size ( $B_J(t, \tau)$ ). These haypiles act as a resource reserve, which is critical for their over-winter survival (Smith 1974a, Erb et al. 2014). We also explicitly model the environmental conditions ( $E(t)$ ), specifically snow depth at any point in time. Lastly, we describe a model of plant biomass ( $R(t)$ ) over the course of the growing season.

### 2.1 Between-season dynamics

The between-season dynamics provide the initial conditions for the differential equations used for within-season dynamics. The environment, snow depth, initial condition,  $E(0)$ , is given by a random variable. This variability in initial snow depth is a proxy for timing of spring within a year. Therefore, a smaller  $E(0)$  corresponds to an earlier timing of spring

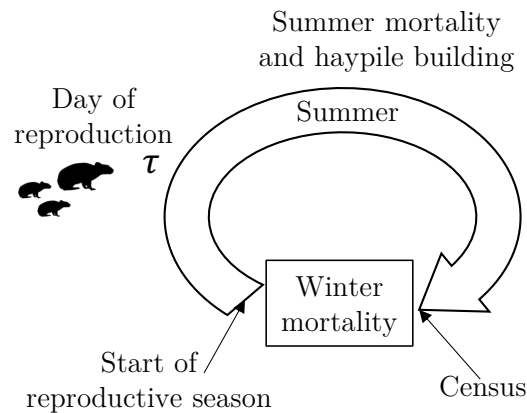


Figure 1: Yearly life-cycle of a pika with major life-history events and modeling components noted. The summer season is modeled using a set of ordinary differential equations (3), section 2.3. A discrete model (1) maps from the end of summer to the start of the next reproductive season, section 2.1. The timing of spring is determined by the snow depth early in the year.

onset. We test several distributions for  $E(0)$ , but use a uniform distribution for most of the analyses. This distribution is centered on a mean value between a minimum,  $a$ , and maximum value  $b$ .

For pikas, we assume that juveniles mature after their first year, and thus become adults if they survive their first winter (White and Smith 2018). Therefore,  $J(0) = 0$  and  $A(0)$  will be the sum of surviving adults and juveniles from the previous year, which is conditional on their haypile size at the start of winter  $B_A(1)$ , and  $B_J(1)$ . The dependence of over-winter mortality on haypile size is defined by the maximum possible over-winter survival rate,  $\sigma$ , and a shape parameter,  $k$ . We assume that the initial resource reserve for both adults and juveniles is zero, a depleted haypile. Lastly, we assume plant biomass is set to an amount just greater than zero to start the year.

Here are the initial values at the beginning of the summer season:

$$\begin{array}{ll}
 \text{Environment:} & E(0) \sim \text{Uniform}(a, b), \\
 \text{Adult density:} & A_{n+1}(0) = A_n(1) \frac{\sigma_A B_A(1)}{k_A + B_A(1)} + J_n(1, \tau) \frac{\sigma_J B_J(1)}{k_J + B_J(1)}, \\
 \text{Juvenile density:} & J_{n+1}(0) = 0, \\
 \text{Adult resource reserve:} & B_A(0) = 0, \\
 \text{Juvenile resource reserve:} & B_J(0) = 0, \\
 \text{Resource:} & R(0) = R^{ini}.
 \end{array} \tag{1}$$

## 2.2 Birth events and reproductive strategies

In our model, we assume a birth pulse, so that an adult can only have one cohort of offspring per year. In other words, all juveniles from a single mother are born at the same time. The average per capita reproductive output  $\alpha$  is estimated from field data (Table 1). The time  $\tau$  at which the juveniles are born is determined by the reproductive strategy of the mother. More general reproductive schedules could be used for different species (Eskola 2009). In principle, the juvenile haypile size  $B_J(\tau)$  at birth could be dependent of the mother's resource reserve, thus maternal effects could be allowed. In our model, we assume the initial juvenile resource reserve to be equal to zero, corresponding to an empty haypile. These assumptions produce the following equations for number of births and the resource reserve:

$$\begin{aligned} \text{Births of juveniles:} & & J(\tau) & = & \alpha A(\tau), \\ \text{Juvenile resource reserve at birth:} & & B_J(\tau) & = & 0 \end{aligned} \quad (2)$$

Juveniles born early in the year have a long time to collect resources, whereas juveniles born later can avoid potentially harsh winter conditions and high mortality, so that the timing of reproduction involves a trade-off (Morrison et al. 2009). It is not known which cues pikas use to determine their timing of reproduction. In other small mammals, photoperiod, temperature, and precipitation have been proposed as possible cues (Bronson 2009). We investigate two kinds of potential reproductive strategies: 1) a timing cue and 2) an environmental cue. In the first case, the day of the year of reproduction  $\tau$  is directly the evolving strategy, corresponding to photoperiod as a cue. We know from the field (Franken and Hik 2004b) that the timing of reproduction for pikas varies from year to year depending on environmental conditions. This weakens the case for photoperiod being the primary cue. Therefore, as a second case we consider such reproductive strategies, in which reproduction happens immediately after the snow depth drops below a threshold (Fig. 2), which is the evolving strategy.

## 2.3 Within-season dynamics

Here  $E(t)$  decays at a rate  $\delta$  through the course of the season. Both  $A(t)$  and  $J(t)$  decrease during the course of the season according to specific mortality rates (Table 1). The juvenile within-season mortality rate depends on  $E(t)$  and three parameters:  $u_J$  (mortality rate when no snow is present),  $u_E$  the maximum mortality rate from snow, and  $K$  (the half-saturation constant for the saturating function for the relationship for mortality and snow depth). Thus, if there is more early season snowfall, juveniles will have a higher mortality rate. For simplicity we use a Holling-type I functional response for pika resource acquisition with  $a$  representing the attack rate. The haypile size also decays at a rate  $\beta$ . Lastly, the plant biomass is assumed to exhibit logistic growth and is consumed by both adults and juveniles according to the type I functional response for resource acquisition. The specific parameter

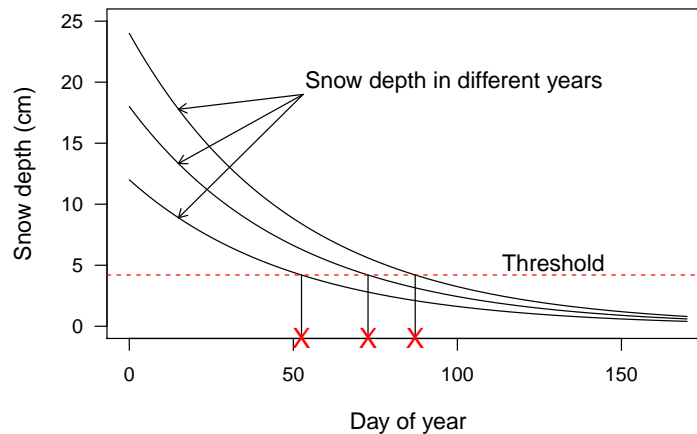


Figure 2: Reproduction strategy based on an environmental cue. The curves represent the amount of snow on the ground (cm) during the reproductive season in different years. The initial snow level is stochastic, but decay occurs deterministically. Adults reproduce when the snow level drops below the threshold strategy value. In contrast with the timing cue, one reproduction strategy based on an environmental cue generates different realized birth dates on different years.

values used in the following set of equations are described in Table 1:

$$\begin{aligned}
 \text{Snow depth:} & \quad \frac{d}{dt} E(t) &= -\delta E(t), \\
 \text{Adult density:} & \quad \frac{d}{dt} A(t) &= -u_A A(t), \\
 \text{Juvenile density:} & \quad \frac{d}{dt} J(t) &= -(u_J + u_E \frac{E(t)}{K+E(t)}) J(t), \\
 \text{Adult haypile size:} & \quad \frac{d}{dt} B_A(t) &= w_A \frac{a_A R(t)}{1+a_A h_A R(t)} - \beta_A B_A(t), \\
 \text{Juvenile haypile size:} & \quad \frac{d}{dt} B_J(t, \tau) &= w_J \frac{a_J R(t)}{1+a_J h_J R(t)} - \beta_J B_J(t), \\
 \text{Plant biomass:} & \quad \frac{d}{dt} R(t) &= r R(t) \left(1 - \frac{R(t)}{K_R}\right) - A(t) \frac{a_A R(t)}{1+a_A h_A R(t)} - J(t) \frac{a_J R(t)}{1+a_J h_J R(t)}
 \end{aligned} \tag{3}$$

## 2.4 Model calibration

We apply our model to a population of the collared pika (*Ochotona collaris*) located in the Ruby Ridge Mountains, Yukon Territory (61° 12' N, 138° 16' W; 1800-2000m). Importantly, this site has been extensively studied since 1995 (Morrison et al. 2009, COSEWIC 2011) with particular work on reproductive timing (Franken and Hik 2004b). Therefore appropriate data exists to parameterize most of our model. The study site is approximately 4 km<sup>2</sup> with 27 distinct talus patches, which is important as the collared pika is an obligate talus dweller (Franken and Hik 2004b). Since 1995, pikas have been live-trapped and given unique identifying tags (Franken and Hik 2004b). A population viability analysis at the Ruby Ridge site estimated a probability of 0.06-0.11 of quasi-extinction by 2029, even in the absence of

climate change (COSEWIC 2011). More information on the specific data collection methods is given in Franken and Hik (2004b) and Morrison et al. (2009).

We attempted to fully specify this model for the pika population at Ruby Ridge mountain range (Table 1). We were able to provide rough estimates of these parameters based on past work at this particular study site and from a related species *Ochotona princeps*. We use environmental data from an Environment Canada weather station at Burwash Landing (61° 22' N, 138° 03' W). This station is lower in elevation (800 m) than the study site, but the regional trends should still be useful (Morrison et al. 2009). We provide more detail in the appendix (Section S1) on how we estimated these parameters. Several parameter estimates are only a rough approximation, therefore we also conducted a parameter sensitivity analysis (Figs. S5-S10).

## 2.5 Adaptive dynamics theory

We have detailed a specific ecological model for within- and between-season population dynamics. Next, we use the framework of adaptive dynamics (Metz et al. 1992; 1996, Geritz et al. 1997; 1998) to study the evolution of reproductive timing (Parvinen et al. 2006, Eskola 2009). We examine evolutionary games between a resident strategy and a mutant, or invader, strategy. A mutant has a different value for the trait of interest, the evolvable trait, compared to the resident population. In our model, we study the evolution of the reproductive strategy, as described in section 2.2. The outcome of these evolutionary games represents a balance of selective pressures from the timing of spring, but also from density- and frequency-dependence. Thus, the outcome does not tell us if plastic or evolutionary responses will be fast enough to keep up with climate change. Instead, the model outcome provides information on the direction plasticity and evolution should drive reproductive timing.

Invasion fitness is the long-term exponential growth rate of a mutant phenotype in an environment set by the resident (Metz et al. 1992). When rare, the mutant has no effect on the local conditions (e.g. resource availability), thereby simplifying the model structure. If fitness is greater than one (because it is a discrete time model), then the mutant is able to invade. Mutations are assumed to be rare enough, so that a resident population is at a population-dynamical steady state when a mutation occurs. This implies a time-scale separation between ecological and evolutionary dynamics (Diekmann 2004, Brännström et al. 2013). Interestingly, monomorphic evolution can be stabilizing, leading into an evolutionarily stable strategy, or disruptive, resulting in a polymorphic population via evolutionary branching (Geritz et al. 1997).

## 3 Results

For a deterministic (non-random environment) scenario, our model predicts an equilibrium attractor, where the starting density of adults is the same at the beginning of each summer season (Fig. 3c). More complicated dynamics (e.g. cycles) arise when stronger nonlinearities are present, particularly in the functional responses. Haypile size increases for both juvenile and adult pikas prior to the onset of winter (Fig. 3d).

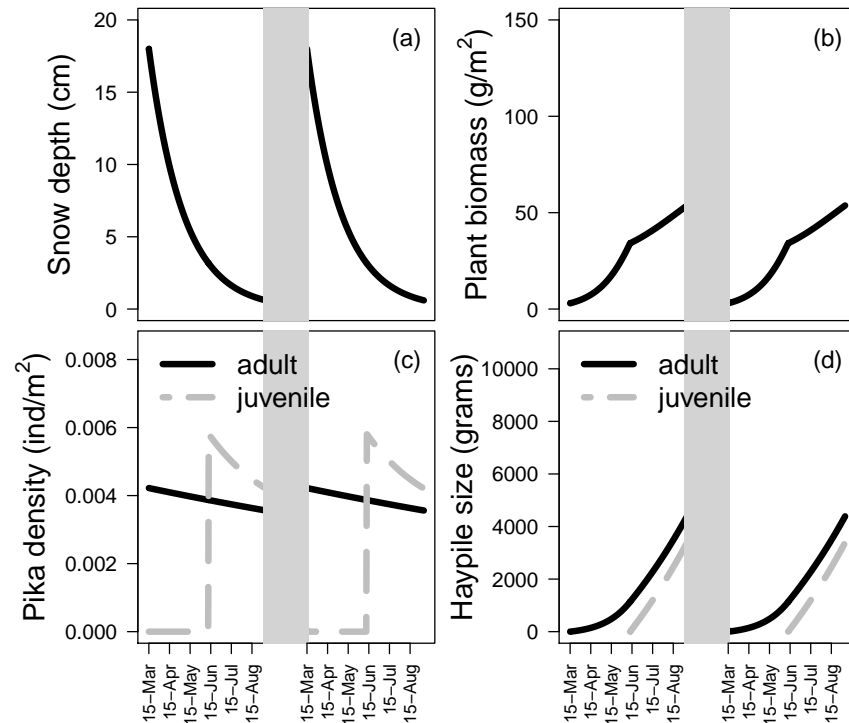


Figure 3: Population dynamics in steady state across two years. Panels show (a) snow depth, (b) plant biomass, (c) adult and juvenile pika density, and (d) adult and juvenile haypile size with respect to within-season time. The gray shaded boxes denote the winter season. Parameter values used are from Table 1. Here the environmental cue is used.

### 3.1 Competing selective pressures result in mid-season reproductive timing

For default parameter values (Table 1) and a deterministic environment, our model predicts an intermediate timing of reproduction, mid-breeding season (Figs. 3, 4). The timing of reproduction is affected by different selective pressures (Eskola 2009). High juvenile mortality at the beginning of the breeding season due to harsh environmental conditions (Millar 1974, Smith 1978) favors later reproduction. In contrast, reproduction late in the season would prevent the juveniles from having sufficient time to collect resources that contribute to their survival over winter (Smith 1978, Morrison et al. 2009), favoring earlier reproduction. The time needed for resource acquisition is accentuated by the competition for resources that occurs during a relatively short summer.

### 3.2 Earlier spring timing selects for earlier reproductive timing

We first considered the evolution of timing of reproduction under constant timing of spring. In such a situation, the initial snow level  $E(0)$  on March 15th is the same in all years, and earlier timing of spring corresponds to a smaller initial snow level  $E(0)$ . We found that earlier spring timing selects for earlier reproductive timing, for both cues (Fig. 4). In case



of the environmental cue, smaller initial snow level results in a smaller evolutionarily stable snow threshold strategy (Figs. 4a), translating into earlier timing of reproduction (Figs. 4b). Analogously, for the timing based cue, an earlier onset of spring selects for an earlier timing of reproduction (Figs. 4c).

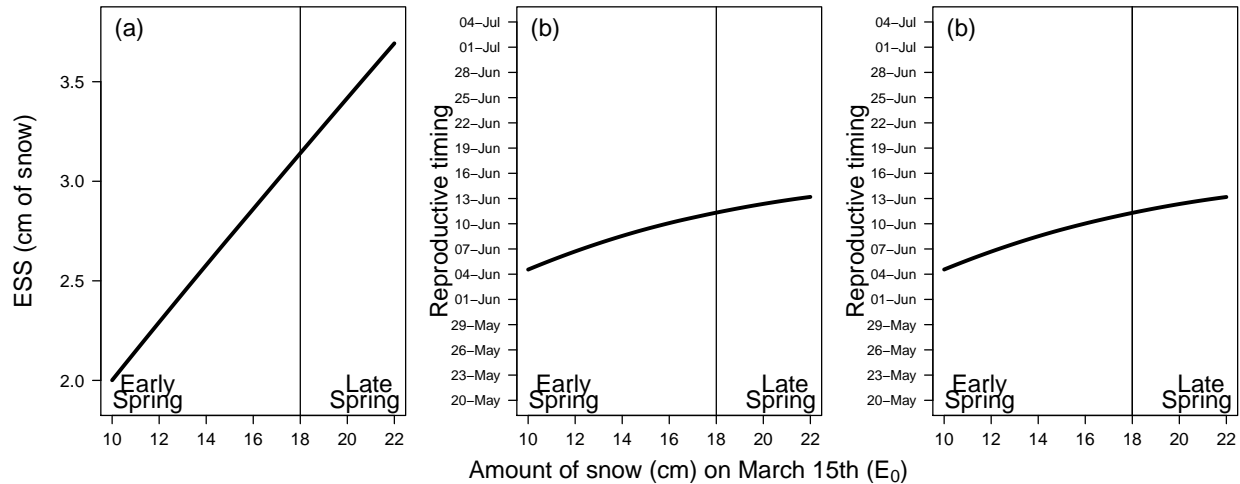


Figure 4: Selection for earlier reproductive timing with earlier spring timing (based on the amount of snowfall on March 15th,  $E_0$ ). (a) Evolutionarily stable strategy (ESS, in centimeters of snow) for environmental cue. (b) Resulting timing of reproduction at the ESS for the environmental cue (c) ESS and predicted reproductive timing for the timing cue. The vertical line on each panel represents the average snow depth in centimeters.

In the deterministic case, there is one-to-one correspondence between the within-year snow level and within-year time. Therefore, one is a completely reliable indicator of the other, and therefore the predicted reproductive timing is the same for both cues (Figs. 4b,c).

### 3.3 More variable spring timing selects for earlier reproductive timing

When the initial snow level varies stochastically each year, the two cues are no longer equivalent, and different evolutionary outcomes are expected. Here we have assumed that the initial snow-level has a uniform distribution  $\text{Uniform}(a, b)$ . For the environmental cue, variability of spring (i.e. variability in  $E(0)$ ) appears to have no significant effect on the ESS snow threshold strategy (Fig. 5a). However, this does translate into earlier reproductive timing with increased variability (Fig. 5b). For the timing cue, increased variability also selects for an earlier timing of reproduction (Fig. 5c), but to a lesser degree compared to the environmental cue. These results were not affected by the choice of distribution for the initial snow-level (Fig. S4).

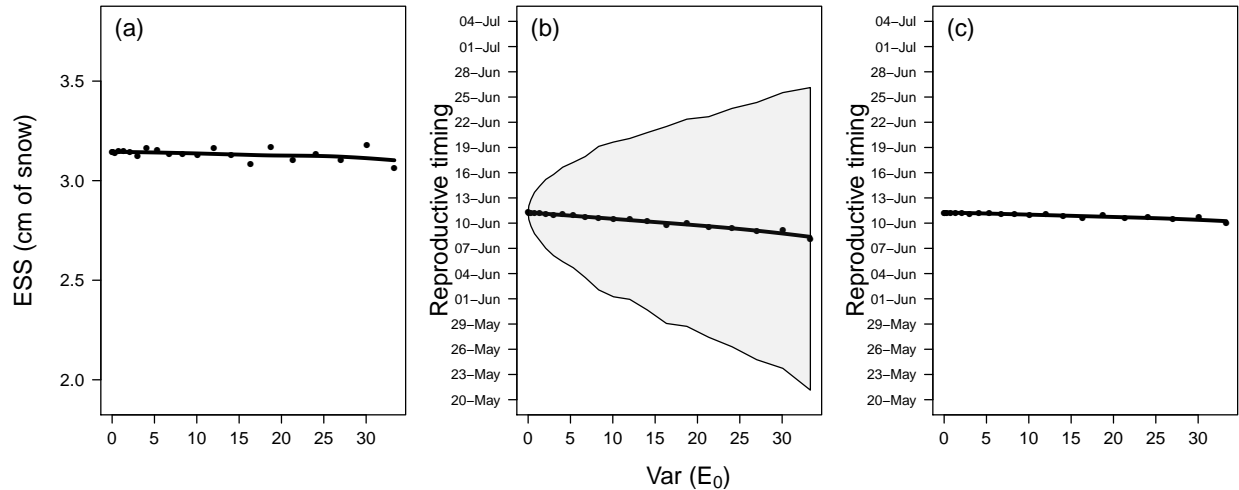


Figure 5: More variable spring timing selects for earlier reproductive timing. (a) Evolutionarily stable snow threshold strategy for the environmental cue. (b) Resulting average timing of reproduction at the ESS (c) Evolutionarily stable reproduction time strategy for the timing cue. In all panels, the mean of  $E(0)$  is held constant at 18.

### 3.4 Altering life-history traits can have opposing selective pressures to climate change

In addition to altering seasonal regimes, climate change could also have direct effects on specific life-history traits. For instance, late season snowstorms could increase mortality rates of juveniles (Morrison and Hik 2007, Smith and Ivins 1983). In our model,  $u_E$  represents the mortality rate of juvenile pikas related specifically to environmental conditions, specifically snow depth. It is conceivable that  $u_E$ , or other life-history parameters, may not be static and could have either plastic or evolutionary responses. We found that increasing  $u_E$  selects for later reproductive timing (Fig. 6). In other words, higher mortality due to snow early in the season predicts a later timing of reproduction. We also determine the evolutionary outcomes for changes in other life-history traits (Figs. S5-S10)

## 4 Discussion

In line with past work, our model predicts that earlier spring timing will select for earlier timing of reproduction. When we introduced variability in our model, an earlier timing of reproduction was the predicted evolutionary outcome (Fig. 5). This finding is important as evolutionary models of reproductive timing typically ignore the role of environmental variability (Eskola 2009, Johansson et al. 2015, but see Iwasa and Haccou 1994, Lof et al. 2012). Lof et al. (2012) showed that environmental variability can produce an adaptive mismatch between reproductive timing and peak food abundance. Our model differs from their work by explicitly including density- an frequency-dependence in evolution, as opposed to only an optimality model.

Environmental variability, introduced in our model as the amount of early season snow

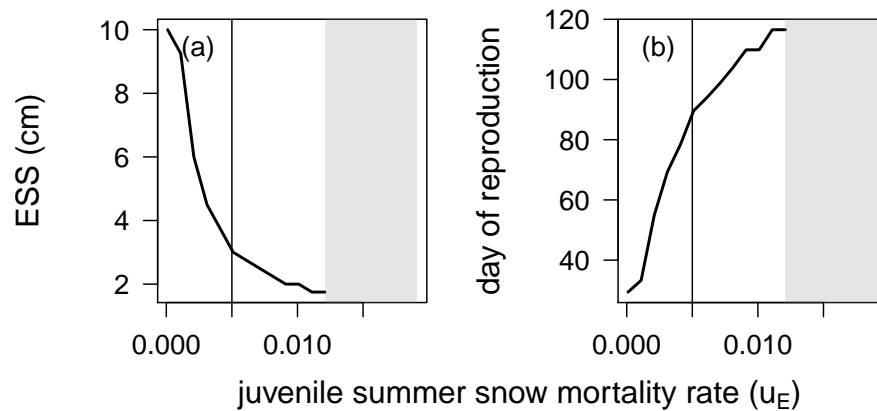


Figure 6: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values juvenile summer mortality with snow present,  $u_E$ . The light grey box indicates value of parameter where the population is not viable. The vertical line is the default parameter value found in Table 1.

depth  $E(0)$ , is an important variable at the Yukon site as it varies dramatically from year-to-year (Fig. S1). Early season snow depth affects the survival rate of juveniles early in the summer. If there was no early-season mortality of juveniles, it would be advantageous for females to reproduce earlier as to allow their offspring more time to collect resources before winter (Morrison et al. 2009). However, given uncertainty about the onset of spring, the model predicts earlier reproductive timing to avoid missing the opportunity to reproduce at all.

In the Yukon, along with many other areas, climate change is expected to have two main effects on seasonal timing. First, and most commonly discussed, is the earlier timing of spring and the subsequent earlier timing of biological activity (Forrest and Miller-Rushing 2010). Morrison and Hik (2007) argue that an earlier snowmelt could benefit pikas by allowing more time for plant growth. Second, climate change is expected to increase the variability in timing of spring onset (ACIA 2005). Our model predicts the most advantageous reproductive timing under future predictions of climate change. However, it does not address whether or not plasticity and evolution will be able to keep up with the pace of climate change (Hoffmann and Sgrò 2011, Boutin and Lane 2014). Our work shows that variability in spring timing will cause additional selective pressures that may make it more difficult for populations to adapt.

At the Yukon site, pikas, on average, reproduce on June 18th, but this varies between June 5th and July 2nd (Franken and Hik 2004b). This strongly suggests pikas use a cue based on environmental conditions (Franken and Hik 2004b). Unfortunately, we do not know what cues pikas actually use to determine their phenology. This is true for most small mammals, but both photoperiod (a timing based cue) and cues based on environmental conditions have been suggested (Bronson 2009). It has been further suggested that small mammals at high latitudes should use photoperiod to determine their phenology (Bronson 2009). However, this is in contrast to what we see in pikas. Although disruptions in seasonal patterns has been documented for many species (Parmesan 2006), it is still unclear how they should respond to a changing climate. This highlights the importance of identifying which

cues organisms use, how the reliability of these cues may be changing, and to see if plasticity or genetic evolution will be fast enough to overcome the effects of climate change (Merilä and Hendry 2014).

We have built general eco-evolutionary framework that incorporates state structure, physiology, and environmental variables. The model is flexible in its applications, but has several important simplifications. Because of the timescale separation between ecology and evolution in the adaptive dynamics framework, we were not able to assess specific predictions of how climate change would affect phenological evolution on a specific time-scale (Diekmann 2004, Brännström et al. 2013). Instead, we obtained information on the most favorable reproductive strategies for climate change scenarios. Our results do not tell us if pikas will actually be able to overcome these selective pressures or on what timescale. In order to better understand an organism's response to climate change, we need information on the current genetic variability, how genetics affects phenological timing, what cues pikas use to determine reproduction, and how climate change affects these cues (Hoffmann and Sgrò 2011). As another simplification, we do not model the phenology of plant growth and instead assume plants begin to grow at the same time each year. In addition, our model of snowfall is governed by simple exponential decay. In the future, it would be interesting to couple a detailed resource-consumer model with a realistic snowfall model.

Our work demonstrates the existence of several selective pressures for phenological timing under future climate change scenarios. There has been a lot of literature documenting earlier timing of reproduction driven by climate change (Forrest and Miller-Rushing 2010), but less work on the role of increased variability in climatic factors (Smith 2011). Our model predicts differ evolutionary outcomes depending on the cue used; this highlights the importance of studying cues for predicting species responses to climate change. Our work also provides some insight into a species that may already be affected by climate change (COSEWIC 2011). The model predicts selection for earlier reproductive timing, but we do not yet know if pikas will be able to keep up with these seasonal changes. Without an understanding of how climate variability can affect selective pressures, we will not know if populations are keeping up with rapid environmental change.

## 5 Author contributions

E.R.W., K.P., and U.D. conceived of the project, designed the models, and wrote the manuscript. E.R.W. programmed and analyzed the models.

## 6 Acknowledgments

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## 7 Supplementary material

An expanded methods section for pikas specifically, model parameterization, sensitivity analyses, and additional results are available online. The code used in this paper and the supplementary material are available at <https://github.com/erwhite1/pika-reproductive-timing>.

## References

- ACIA. Arctic Climate Impact Assessment - Scientific Report. Technical report, 2005.
- Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F., and Mote, P. W. Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology*, 17(6): 2054–2070, 2011. ISSN 13541013. doi: 10.1111/j.1365-2486.2010.02389.x.
- Boutin, S. and Lane, J. E. Climate change and mammals: Evolutionary versus plastic responses. *Evolutionary Applications*, 7(1):29–41, 2014. ISSN 17524563. doi: 10.1111/eva.12121.
- Brännström, Å., Johansson, J., and von Festenberg, N. The hitchhiker’s guide to Adaptive Dynamics. *Games*, 4:304–328, 2013. ISSN 2073-4336. doi: 10.3390/g4030304.
- Bronson, F. H. Climate change and seasonal reproduction in mammals. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 364(1534):3331–40, 2009. ISSN 1471-2970. doi: 10.1098/rstb.2009.0140.
- Childs, D. Z., Metcalf, C. J. E., and Rees, M. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B*, 277(1697):3055–64, oct 2010. ISSN 1471-2954. doi: 10.1098/rspb.2010.0707.
- COSEWIC. COSEWIC assessment and status report on the Collared Pika (*Ochotona collaris*) in Canada. Technical report, Committee on the Status of Endangered Wildlife in Canada, Ottawa, 2011.
- Dearing, M. D. The function of haypiles of pikas. *Journal of Mammalogy*, 78(4):1156–1163, 1997.
- Diekmann, O. A beginner’s guide To adaptive dynamics. *Banach Center Publications*, 63: 47–86, 2004.
- Erb, L. P., Ray, C., and Guralnick, R. Determinants of pika population density vs. occupancy in the Southern Rocky Mountains. *Ecological Applications*, 24(3):429–435, 2014. ISSN 10510761. doi: 10.1890/13-1072.1.
- Eskola, H. T. On the evolution of the timing of reproduction. *Theoretical Population Biology*, 75(2-3):98–108, 2009. ISSN 00405809. doi: 10.1016/j.tpb.2008.12.001.
- Forrest, J. and Miller-Rushing, A. J. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555):3101–3112, 2010. ISSN 0962-8436. doi: 10.1098/rstb.2010.0145.

- Franken, R. J. and Hik, D. S. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *Journal of Animal Ecology*, 73(5):889–896, 2004a. ISSN 00218790. doi: 10.1111/j.0021-8790.2004.00865.x.
- Franken, R. J. and Hik, D. S. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the Southwest Yukon. *Integrative and Comparative Biology*, 44(2):186–93, 2004b. ISSN 1540-7063. doi: 10.1093/icb/44.2.186.
- Geritz, S. A., Kisdi, É., Meszéna, G., and Metz, J. A. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1): 35–57, 1998. ISSN 02697653. doi: 10.1023/A:1006554906681.
- Geritz, S., Metz, J., Kisdi, É., and Meszéna, G. Dynamics of Adaptation and Evolutionary Branching. *Physical Review Letters*, 78(10):2024–2027, 1997. ISSN 0031-9007. doi: 10.1103/PhysRevLett.78.2024.
- Gienapp, P., Lof, M., Reed, T. E., McNamara, J., Verhulst, S., and Visser, M. E. Predicting demographically sustainable rates of adaptation: can great tit breeding time keep pace with climate change? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368(1610):20120289, 2013. ISSN 1471-2970. doi: 10.1098/rstb.2012.0289.
- Hoffmann, A. and Sgrò, C. Climate change and evolutionary adaptation. *Nature*, 470(7335): 479–485, 2011. ISSN 1476-4687. doi: 10.1038/nature09670.
- Iwasa, Y. and Haccou, P. ESS emergence pattern of male butterflies in stochastic environments. *Evolutionary Ecology*, 8(5):503–523, 1994. ISSN 02697653. doi: 10.1007/BF01238255.
- Johansson, J. and Jonzén, N. Effects of territory competition and climate change on timing of arrival to breeding grounds: a game-theory approach. *The American Naturalist*, 179(4):463–74, 2012. ISSN 1537-5323. doi: 10.1086/664624.
- Johansson, J., Kristensen, N. P., Nilsson, J. Å., and Jonzén, N. The eco-evolutionary consequences of interspecific phenological asynchrony - a theoretical perspective. *Oikos*, 124(1):102–112, 2015. ISSN 16000706. doi: 10.1111/oik.01909.
- Lof, M. E., Reed, T. E., McNamara, J. M., and Visser, M. E. Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. *Proceedings of the Royal Society B*, 279(1741):3161–3169, 2012. ISSN 0962-8452. doi: 10.1098/rspb.2012.0431.
- Mailleret, L. and Lemesle, V. A note on semi-discrete modelling in the life sciences. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 367(1908):4779–4799, 2009. ISSN 1364503X. doi: 10.1098/rsta.2009.0153.

- McIntire, E. J. B. and Hik, D. S. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. *Oecologia*, 145(2):288–297, 2005. ISSN 00298549. doi: 10.1007/s00442-005-0127-z.
- Merilä, J. and Hendry, A. P. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. *Evolutionary Applications*, 7(1):1–14, 2014. ISSN 17524563. doi: 10.1111/eva.12137.
- Metz, J., Nisbet, R., and Geritz, S. How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, 7(6):198–202, 1992.
- Metz, J. a. J., Geritz, S. a. H., Meszner, G., Jacobs, F. J. a., and van Heerwaarden, J. S. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. *Stochastic and Spatial Structures of Dynamical Systems. Proceedings of the Royal Dutch Academy of Science*, (September):183–231, 1996.
- Millar, J. C. Success of reproduction in pikas, *Ochotona princeps*. *Journal of Mammalogy*, 55(3):527–542, 1974. doi: 10.1644/870.1.Key.
- Morrison, S. F. and Hik, D. S. Demographic analysis of a declining pika *Ochotona collaris* population: Linking survival to broad-scale climate patterns via spring snowmelt patterns. *Journal of Animal Ecology*, 76(5):899–907, 2007. ISSN 00218790. doi: 10.1111/j.1365-2656.2007.01276.x.
- Morrison, S. F., Pelchat, G., Donahue, A., and Hik, D. S. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia*, 157(1): 107–116, 2009. ISSN 00298549. doi: 10.1007/s00442-008-1.
- Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37:637–669, 2006.
- Parvinen, K., Dieckmann, U., and Heino, M. Function-valued adaptive dynamics and the calculus of variations. *Journal of Mathematical Biology*, 52:1–26, 2006. doi: 10.1007/s00285-006-0020-3.
- Roland, J. and Matter, S. F. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. *Ecology*, 94(1):190–199, 2013. ISSN 00129658. doi: 10.1890/12-0611.1.
- Smith, A. T. The distribution and dispersal of pikas: Consequences of insular population structure. *Ecology*, 55(5):1112–1119, 1974a.
- Smith, A. T. The distribution and dispersal of pikas: influences of behavior and climate. *Ecology*, 55(6):1368–1376, 1974b.
- Smith, A. T. Comparative demography of pikas (*Ochotona*): Effect of spatial and temporal age-specific mortality. *Ecology*, 59(1):133–139, jan 1978.

- Smith, A. T. and Ivins, B. L. Reproductive tactics of pikas: why have two litters? *Canadian Journal of Zoology*, 61(Severaid 1950):1551–1559, 1983. ISSN 0008-4301. doi: 10.1139/z83-209.
- Smith, A. T. and Ivins, B. L. Spatial relationships and social organization in adult pikas - a facultatively monogaous mammal. *Zeitschrift fur Tierpsychologie*, 66:289–308, 1984.
- Smith, A. T. and Nagy, J. D. Population resilience in an American pika (*Ochotona princeps*). *Journal of Mammalogy*, 96(2):393–404, 2015. ISSN 1545-1542. doi: 10.1093/jmammal/gyv040.
- Smith, A. T. and Weston, M. L. *Ochotona princeps*. *Mammalian Species*, 352:392–397, 1990.
- Smith, M. D. An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, 99(3):656–663, 2011. ISSN 00220477. doi: 10.1111/j.1365-2745.2011.01798.x.
- Stevenson, T. J., Visser, M. E., Arnold, W., Barrett, P., Biello, S., Dawson, A., Denlinger, D. L., Dominoni, D., Ebling, F. J., Elton, S., Evans, N., Ferguson, H. M., Foster, R. G., Hau, M., Haydon, D. T., Hazlerigg, D. G., Heideman, P., Hopcraft, J. G. C., Jonsson, N. N., Kronfeld-Schor, N., Kumar, V., Lincoln, G. A., Macleod, R., Martin, S. A. M., Martinez-Bakker, M., Nelson, R. J., Reed, T., Robinson, J. E., Rock, D., Schwartz, W. J., Steffan-Fewenter, I., Tauber, E., Thackeray, S. J., Umstatter, C., Yoshimura, T., and Helm, B. Disrupted seasonal biology impacts health, food security and ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 282:20151453, 2015. ISSN 0962-8452. doi: 10.1098/rspb.2015.1453.
- Visser, M. E. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 275(1635):649–659, 2008. ISSN 09628452 (ISSN). doi: 10.1098/rspb.2007.0997.
- White, E. R. and Hastings, A. Seasonality in ecology: Progress and prospects in theory. *PeerJ Preprints*, 6(e27235v1), 2018.
- White, E. R. and Smith, A. T. The role of spatial structure in the collapse of regional metapopulations. *Ecology*, 2018. doi: <https://doi.org/10.1002/ecy.2546>.
- Wilkening, J. L., Ray, C., Beever, E. A., and Brussard, P. F. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International*, 235(1-2):77–88, 2011. ISSN 10406182. doi: 10.1016/j.quaint.2010.05.004.



Notation	Description	Units	Estimate	Reference
$\delta$	Decay parameter for snow depth	1/day	0.02	Environment Canada
$E(0)$	Average snow depth on March 15th	cm	18.00	Environment Canada
$\sigma_E$	Standard deviation of snow depth on March 15th	cm	12.00	Environment Canada
$u_A$	Adult mortality rate	1/day	-0.001	COSEWIC (2011), Appendix S1
$u_J$	Summer mortality rate of juveniles with no snow present	1/day	-0.001	Appendix S1
$u_E$	Maximum summer mortality rate of juveniles with snow present	1/day	-0.005	Appendix S1
$K$	Half-saturation constant for $E[t]/(K + E[t])$	cm	1	Appendix S1
$w_J$	Conversion of resources into resource reserve	none	0.33	Smith and Ivins (1984)
$\beta_J$	Decay of resource reserve	1/day	-0.0015	Dearing (1997)
$w_A$	Conversion of resources into resource reserve	none	0.33	Smith and Ivins (1984)
$\beta_A$	Decay of resource reserve	1/day	-0.0015	Dearing (1997)
$r$	Intrinsic rate of growth	1/day	0.044	McIntire and Hik (2005)
$K_R$	Carrying capacity	grams/m <sup>2</sup>	150.00	McIntire and Hik (2005)
$a_A$	Per-capita adult attack rate	m <sup>2</sup> /day/adult	3	Appendix S1
$a_J$	Per-capita juvenile attack rate	m <sup>2</sup> /day/juvenile	3	Appendix S1
$\sigma_A$	Max adult over winter survival	none	0.90	COSEWIC (2011)
$K_A$	Half saturation constant for adult over winter survival	grams	2500	Morrison et al. (2009)
$\sigma_J$	Max juvenile over winter survival and maturation probability	none	0.90	COSEWIC (2011)
$K_J$	Half saturation constant for juvenile over winter survival and maturation probability	grams	2500	Morrison et al. (2009)
$s(t)$	Number of female offspring per adult each year	$\frac{\text{female offspring}}{\text{female}}$	1.50	Smith and Weston (1990)

Table 1: Default model parameters derived from literature or calculated in Appendix S1 for the Collared pika (*Ochotona collaris*) population at Ruby Ridge, Yukon, Canada.