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

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All code for these plots and those found in the manuscript can be found at www.github.com/erwhite1/pika-reproductive-timing

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S1 Model parameterization

S1.1 Environment

For the collared pika in the Yukon, timing of snowmelt and the amount of snow accumulation appear to be important factors for the timing of reproduction (Morrison and Hik 2007). We assume the environment, specifically the amount of snow (cm) on the ground, is a decay process where snow melts over the course of the year. The initial condition is therefore the amount of snow present at the beginning of the season, which is arbitrarily set at March 15th. Unfortunately, there does not exist good environmental data at the study site at Ruby Range (see main text) and we instead use weather information from the Environment Canada weather station at Burwash Landing (61° 22'N, 139° 3'W). Therefore the weather information is useful in a relative sense regarding the amount of snow and timing of snowmelt at the study site (Morrison et al. 2009).



snow on ground (cm) on March 15th

Figure S1: Frequency of the amount of snow present (cm) on the ground on March 15th of each year from 1989-2014. The data is from Environment Canada Burwash A station.



Time since March 15th

Figure S2: Fitted curves for the change in snow depth since March 15th of each year. The intercept is held constant for each curve fit.

Assuming a constant rate of decay in snow depth, we estimated the decay parameter, $\epsilon = -0.0234278$, using data on daily snow depth over the past two decades. We estimated a mean snow depth (E_0) on March 15th to equal 18.48.

S1.2 Birth rate

Past work has indicated that pikas in the Yukon have one litter per year (Franken and Hik 2004) of between 2.1 and 3 individuals (Smith and Weston 1990). In our model, we assume a birth pulse. Therefore, each female has all of her offspring within a given year at the same time. Thus, the number of offspring born in a year is simply the average number of female offspring (i.e. we halve the overall birth rate to 1.5) multiplied by the number of adult females.

S1.3 Adult summer mortality

There are not field estimates of adult summer mortality, but it is thought to be low (J.D. Nagy, personal communication). Between 1995-2009, COSEWIC (2011) estimated a yearly mortality rate of 0.63 for female adult pikas. We assume a modest percentage of mortality occurs in summer, around 0.15, or a quarter of the yearly mortality rate. We can use this estimate and solve for u_A in the within season equation for adults, we obtain an estimate $u_A = -0.001$.

S1.4 Juvenile summer mortality

There are often high rates of mortality for juveniles after birth (Millar 1974). In addition, pikas are known to abandon entire litters if weather conditions are poor. Both of these processes act early in the reproductive season. However, little is known about either process for our particular species of interest. For a related species, *Ochotona princeps*, 21% of offspring may die before weaning occurs (Millar 1974).

We assume a juvenile summer mortality function that is affected by current environmental conditions in equation 1 of the main manuscript. Here, u_J is the summer mortality rate for juveniles when there is no snow present, optimal environmental conditions. Then, $u_E + u_J$ is the maximum mortality rate when there is a lot of snow present. Lastly, K is the half saturation constant, or the amount of snow at which there is $u_E/2$ mortality rate, that determines the shape of the saturating curve between mortality and E(t).

Unfortunately, there are no published estimates of of these specific parameters as juveniles are only captured several months after they are born (Franken and Hik 2004). Weaning mortality occurs between birth and the time of first capture. Therefore, we used the difference between number of juveniles captured each year (COSEWIC 2011) and the maximum birth rate, to try and estimate the juvenile summer (or weaning) mortality rate. We found that the weaning mortality rate ranged from 0.27 to 0.76 each year.

First, we assumed that juvenile mortality without snow, u_J , was the same as the adult summer mortality, u_A . Unfortunately, these parameters were non-identifiable due to the limited number of data points to estimate such a complicated function. Therefore, we resorted to using the model itself to estimate u_E and K. In an average snowfall year, a value of $u_E = 0.005$ and K = 1 results in a summer mortality rate of 28%, in line with previous work (Millar 1974).

S1.5 Plant consumption

We assume that plants are consumed by juveniles and adults by Holling type I or type II functional responses. In the model, we describe different functions for juveniles and adults, but we assume they have the same parameter values. In particular, there are two parameters a, the attack rate. And second, if using a type II response is h, the handling time.

In our model, a is the attack rate and is in units area/time as the amount of resources is given as a density. Biologically, a is the amount of area a pika can search during a particular foraging bout. Pikas only travel short distances during foraging bouts. Unfortunately, we do not have an estimate of the foraging area covered by pikas during a single trip. Therefore, we use our model to indirectly estimate a_A , an inverse modeling procedure (White et al. 2014). In order for pikas to achieve the mean grams per haypile found by the end of summer in Morrison et al. (2009), $a_A = 3$.

The handling time is the amount of time required for a pika to collect 1 gram of plant material. We do not have a direct estimate of handling time, but we can use the maximum number of foraging bouts within an hour to estimate handling time. Each trip takes an estimated 2.4 minutes (Morrison et al. 2009) and results in on average 0.62 grams of plant material. This results in a handling time, h_A of 0.00269 days/gram food.

In the results of the main text, we focus on a linear (type I) functional response when the handling time is zero, this simplifies what attractors are possible.

S1.6 Resource reserve (haypile size)

Through resource consumption, as described in the previous section, and the use of those resources, a resource reserve, or happile size, can either increase or decrease. We assume resources collected during foraging are converted into a resource reserve, in this case happile size, at a rate determined by $w_A = 1/3$ (Smith and Ivins 1984). This rate is calculated as the fraction of time foraging spent having versus the combined time spent having and feeding.

S1.7 Resource decay

We assume resources, or happile size, decays at a constant rate. Dearing (1997) constructed eight artificial happiles in West Knoll, Colorado. Dearing (1997) then estimated the amount of biomass loss each month in summer and winter. We use these results to estimate the decay parameter, β , of happile size, B_A . We assume this parameter is the same for both juveniles and adults. In the equation below, 62 is the number of days over which Dearing (1997) estimated happile decay at a study site in Colorado.

$$B_A(t) = B_A(0)e^{\beta_A t}$$
$$7.3 = 8e^{\beta_A 62}$$
$$\beta_A = -0.00147 \frac{grams}{day}$$

This estimation is probably different at the Yukon site given different plant material and environmental conditions, but no similar experiments have been conducted there.

S1.8 Plant growth

Peak vegetation biomass near talus occurs in late July at the study site and senescence begins soon thereafter (McIntire and Hik 2005). From past work, we have estimates of the relative amount of AGB (above ground biomass) in absence of pikas from pika exclusion plots. McIntire and Hik (2005) estimated plant abundance is for four different time points during one summer at the study site. Plant growth increases until July and then declines before winter begins.

We assume plant growth in the absence of predation is governed by a simple logistic growth equation. Therefore, both the intrinsic rate of growth r and the carrying capacity K_R need to be estimated. We use data from the pika-exclusion experiment on plant growth (McIntire and Hik 2005). Although the data is limited, we were able to fit the solution to the logistic growth equation to obtain estimates for r and K_R (Fig. S3). We assume that growth starts from a small amount (3 g/m²) of biomass each spring.



Figure S3: Fit of logistic growth model for plant density data found in McIntire and Hik 2005.

Assuming a logistic equation for plant growth, our model estimated r=0.0443 and $K_R=136.8244$.

S1.9 Over-winter parameterization

Pikas often experience high over-winter mortality (Morrison and Hik 2007). Their survival depends on the size of their happile before winter begins. Therefore, we assumed a saturating function where over-winter survival depends on happile size. Morrison et al. (2009) examined over-winter survival and found it depended on when pikas initiated happing, and thus their happile size. We assume a high potential over-winter survival of 0.9, which is likely rarely achieved as pikas are not able to build large enough happiles most years, but it is just a maximum value. We roughly estimate the half-saturation parameter to be near $k_A = 2500$, based on the probability of survival for pikas over one winter (Morrison et al. 2009).

We assume that all juvenile pikas either become adults (acquiring a territory) or die over winter (Smith and Weston 1990). Therefore, we do not need a function for juvenile over-winter mortality.

S2 Different distributions for spring timing

In the main manuscript, we showed that increased variability in the timing of spring changed selection pressure for the timing of reproduction (Fig. 5). Therefore, we also wanted to explore if different distribution shapes for timing of spring would affect the selection pressures. Here we compare different distributions for the winter snow depth, and thus different times on spring onset. We held the mean and variance of each distribution constant for comparison. We found that the type of noise, the specific shape of the spring timing distribution, did not alter the predicted evolutionarily stable strategy, nor the reproductive timing (Fig. S4).



Figure S4: Evolutionary stable strategy (ESS, centimeters of snow) and average reproductive timing (RT, day of the year) for eight different distributions of the initial snow depth (E_0) on March 15th. All distributions have a mean of 18 and a variance of 10 to allow for comparison. All of these results are for the environmental cue. The results are the same for the timing cue.

S3 Sensitivity analyses

Here we illustrate the sensitivity of the predicted evolutionary stable strategies (ESS) and day of reproductive timing to changes in parameter values. Assuming no environmental stochasticty, we varied parameters away from defaults (see Table 1 in main text) and then determined the ESS and realized reproductive timing. We specifically examined the juvenile mortality parameters as these were not estimated from field data. Additionally, we examined the birth rate and over-winter mortality rate because of their importance in determining evolutionary outcomes.



Figure S5: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values of birth rate (litter size). 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 of the main text.



Figure S6: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values juvenile summer mortality with no snow present, u_J . 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 of the main text.



Figure S7: (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 of the main text.



Figure S8: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values juvenile summer mortality half-saturation constant, K. A larger value of K implies pika mortality increases faster with snow depth. 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 of the main text.



Figure S9: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values of attack rate for both juveniles (a_J) and adults (a_A) . 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 of the main text.



Figure S10: (a) Predicted evolutionary stable strategy and (b) day of reproduction for different values of maximum over-winter survival rate for both juveniles (σ_J) and adults (σ_A). 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 of the main text.

S4 References

COSEWIC. 2011. COSEWIC assessment and status report on the Collared Pika (Ochotona collaris) in Canada. Page 50. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Dearing, M. D. 1997. The function of happiles of pikas. Journal of Mammalogy 78:1156–1163.

Franken, R. J., and D. S. Hik. 2004. Interannual variation in timing of parturition and growth of collared pikas (Ochotona collaris) in the Southwest Yukon. Integrative and Comparative Biology 44:186–93.

McIntire, E. J. B., and D. S. Hik. 2005. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. Oecologia 145:288–297.

Millar, J. C. 1974. Success of reproduction in pikas, Ochotona princeps. Journal of Mammalogy 55:527–542.

Morrison, S. F., and D. S. Hik. 2007. Demographic analysis of a declining pika Ochotona collaris population: Linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76:899–907.

Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 157:107–116.

Smith, A. T., and B. L. Ivins. 1984. Spatial relationships and social organization in adult pikas - a facultatively monogaous mammal. Zeitschrift fur Tierpsychologie 66:289–308.

Smith, A. T., and M. L. Weston. 1990. Ochotona princeps. Mammalian Species 352:392–397.

White, E. R., J. D. Nagy, and S. H. Gruber. 2014. Modeling the population dynamics of lemon sharks. Biology Direct 9:1–18.