Delayed Parturition Determined by Body Condition: A State-Dependent Life History Model for Elk

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Abstract

The long-lived iteroparous animals are known to favor their own survival over current reproduction. Indeed, the tradeoff between future survival and investment in reproduction is central to life history theory. One means of managing this tradeoff involves the adjustment of reproductive investment post conception. We modeled one such strategy, using a series of life stage-specific equations (both deterministic and stochastic) derived either from our own empirical data or from previously published data for elk, in which a simulated population of female elk adjust the parturition date of their calves based on their body condition. We predicted that due to the reduced energetic costs of gestation relative to lactation, females would be able to enter winter in a better state and thus more likely to survive to attempt reproduction the following season. In addition, calves would be born larger and thus better able to survive through the summer. These two factors would lead to the simulated elk populations employing this state-dependent "bet-hedging" strategy to increase at a faster rate than populations for which timing of reproduction is independent of maternal condition. Our result supported the prediction that elk simulated using the bet-hedging strategy would have a higher rate of population increase. However, this was driven mostly by female over-winter survival rates. These results help provide a better understanding of the evolution of life-history traits and how they affect population dynamics.

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Dedication

This thesis is dedicated to those who connect reason with creativity and do so to make the world a better place for all

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Introduction

The tradeoff between investment in current reproduction versus future survival (i.e., the 'cost of reproduction' tradeoff) is a central tenet of life-history theory (Stearns 1992, Roff 1993), and long-lived iteroparous animals are well known for favoring their own survival over current reproductive investment (Gaillard et al. 2000, Ellison 2003, Brown and Sibly 2006, Therrien et al. 2008). Although reproductive failure in such animals sometimes manifests in the form of reproductive pauses (Williams 1966, Clutton-Brock et al. 1983, Stearns 1992, Bårdsen et al. 2010), an alternative strategy involves the adjustment of reproductive investment post conception. For example, in capital breeders (Jönsson 1997, Festa-Bianchet et al. 1998, Macdonald, et al. 2020) like North American elk (*Cervus canadensis*), conception occurs nearly every year, but prenatal, perinatal, or neonatal mortality can effectively eliminate most of the costs of reproduction at the 'last minute'. This strategy is facilitated in mammals by the lower cost of gestation relative to lactation (Clutton-Brock et al. 1989); if a maternal female loses her offspring before having to bear the costs of lactation, then the bulk of that year's resources can still be invested in somatic maintenance and growth rather than in reproduction.

Bet-hedging strategies like the one described above are especially advantageous in temperate and arctic environments where maternal condition in autumn serves as a buffer against the energetic stresses of winter (Erikstad et al. 1998; Bårdsen et al. 2008, 2011). Owing to the differential costs of gestation versus lactation, such strategies allow females that conceive in autumn, when winter and spring conditions are still unknown, to effectively delay much of their investment in reproduction to a time when those conditions become known (Gaillard et al. 2000, Bårdsen et al. 2008, Milner et al. 2013). In capital-breeding species, fetuses are often well-buffered against nutritional deficiencies of the dam from the beginning of the second trimester onward (Markgren 1969, Milner et al. 2013), which further helps to facilitate delayed investment in reproduction with low initial risk to offspring. Moreover, although maternal condition often is a predisposing factor for neonatal mortality (Skogland 1984, Clutton-Brock et al. 1987, Keech et al. 2000, Tveraa et al. 2003, Hamel et al. 2010), birth mass of young is typically unrelated to maternal condition at or near parturition (Monteith et al. 2013, Long et al. 2016). This suggests that the predisposing factor is related to reduced investment in lactation rather than gestation.

‘Conservative’ strategies of reproductive allocation typically involve reduced investment in reproduction at conception (e.g., reproductive pauses), gestation, or lactation (Descamps et al. 2016). Although the lower cost of gestation relative to lactation is an important part of what facilitates such strategies in the first place, under the right conditions this difference in the costs of reproduction may also facilitate another, arguably less intuitive, strategy. Those conditions, which are relatively common among capital-breeding ungulates, include:

1. Females have the capacity to adjust gestation length (Clements et al. 2011).
2. Neonatal mortality occurs largely during the first month of life (e.g., Barber-Meyer et al. 2010) and is inversely related to birth mass (Smith and Anderson 1996, Long et al. 2016).
3. The influence of birth mass on the probability of surviving the first month of life is considerably stronger than the influence of autumn body mass on the probability of surviving the first winter of life (Clutton-Brock et al. 1987).

Under these circumstances, a female in poor nutritional condition could potentially increase their fitness by (1) delaying parturition and increasing investment in gestation, (2) giving birth to a correspondingly larger neonate that has a higher probability of survival during its first month of life, and (3) subsequently reducing investment in lactation to help rebuild somatic reserves. Over time, such a state-dependent bet-hedging strategy could potentially result in more young recruited while simultaneously maintaining a high annual probability of survival for the female.

We collected data from adult female elk and their offspring in a temperate montane forest from 2010–2012 as part of an unrelated study. Several relationships observed in those data, however, suggested the existence of state-dependent bet-hedging in the allocation of energy to reproduction. We lacked the sample size to facilitate a rigorous empirical test of this hypothesis, and thus opted instead to develop a series of stochastic simulation models parameterized with our and others' data to evaluate the potential for state-dependent bet-hedging to improve population performance. We used those models to test the following hypothesis:

> **H1**: In capital-breeding ungulates like elk (*Cervus canadensis*), lifetime fitness can be improved via a state-dependent bet-hedging strategy wherein females in poor condition in early spring (1) increase birth mass of their calves by delaying parturition and investing more in fetal growth during the last third of gestation, and (2) reduce investment in lactation following parturition.

Due to the lower cost of gestation relative to lactation, such a strategy could increase both the probability of neonatal survival during early life (which is strongly determined by birth mass) and the probability of dam survival (by facilitating greater allocation of energy to somatic reserves during summer). Conversely, females in good condition in early spring should give birth sooner (on average) and invest more in lactation to foster rapid early growth of their neonates. We predicted that in the absence of other limiting factors, simulated elk populations employing this state-dependent bet-hedging strategy would increase at a faster rate than populations for which timing of reproduction is independent of maternal condition.

Methods and Materials

Study site

Empirical data used to initialize our models were obtained from a variety of sources (see description of model parameterization below). However, the data that had initially suggested the bet-hedging strategy were obtained at the Starkey Experimental Forest and Range (hereafter Starkey; 45.8130 N, 118.8310 W; Figure 1) between 2010 and 2012 (Long et al. 2014, 2016). Starkey is a 101-km^2 research site situated in the Blue Mountains of northeastern Oregon, USA. Starkey is operated by the U.S. Forest Service and is surrounded by a 2.4-m high fence that prevents immigration or emigration of large herbivores (Rowland et al. 1997) but plays no role in habitat selection by elk (Stewart et al. 2002, 2006). The fence also divides Starkey into several distinct research areas; the study that generated our data was conducted in the largest of those which, at 78 km^2 is several times larger than the average home range reported for elk in the Blue Mountains (Leckenby 1984). Starkey supports the highest density of elk in the state of Oregon (estimated between 4.2 and 7.6 elk/km^2; Spitz et al. 2018, Merems et al. 2020), but the population is probably still below carrying capacity (K) based on consistently high pregnancy rates (Noyes et al. 1997), excellent nutritional condition, and large birth mass of young (Kie et al. 2003, Stewart et al. 2005; R. A. Long et al., unpublished data). Traffic levels and recreational activities (e.g., hunting) are similar to patterns of use on nearby public lands (Rowland et al. 1997). Starkey is subject to a dry continental climate; mean maximum temperature recorded by the nearest weather station (maintained by the National Oceanic and Atmospheric Administration; elevation 1102 m) is 13.98°C during spring (April–June), the period when data used in our study were collected (Western Regional Climate Center). Mean total precipitation in spring is 18.4 cm (Western Regional Climate Center). Elevations range from 1120 to 1500 m, and common plant communities included bunchgrasses (*Festuca idahoensis*, *Poa secunda*, *Pseudoroegneria spicata*), ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lodgepole pine (*Pinus contorta*; Long et al. 2008). Primary predators at Starkey are mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*).

During early spring of 2010-2012, 36 adult female elk were captured and fit with GPS collars following methods described by Wisdom et al. (1993) and Long et al. (2014, 2016). Nutritional condition was measured at the time of capture using standard protocols developed for elk, which included measuring maximum depth of rump fat via ultrasonography and assigning a condition score to those animals that had catabolized subcutaneous fat reserves (Cook et al. 2010). Those data were combined with data on body mass to estimate percent ingesta-free body fat (IFBF) for each individual as an overall measure of nutritional condition (Cook et al. 2010).

Pregnancy was also assessed at the time of capture, and pregnant females were fit with a vaginal implant transmitter (VIT) to monitor timing and location of parturition. Each VIT transmitted a temperature-modulated pulse on a unique frequency that indicated the timing of expulsion and, ostensibly, parturition. VITs were monitored daily throughout the birthing season (May–June) via ground-based radiotelemetry. When a birthing event was suspected based on expulsion of a VIT the dam was located by radiotelemetry. If a calf was not seen in the vicinity of the dam then a search was conducted in the immediate area (≤100-m radius). Captured neonates were blindfolded and sex, age and size-related data were collected. Age was estimated to the nearest hour of VIT expulsion or, if expulsion time was not available, morphology and stage of development was compared to known-age neonates. Calves were fitted with ear tags and expandable radio collars that included mortality sensors and were monitored daily through August. When a mortality signal was detected, the collar was located, and verification of mortality was attempted. If no evidence of mortality was found, the collar was assumed to have been slipped and the calf and dam were censored from subsequent analysis. Of the original 36 calves collared, 11 were recaptured in the fall (1 in 2010 and 10 in 2012) during early winter elk handling at Starkey (Wisdom et al. 1993); calf body mass and nutritional condition of the associated dams were measured again at that time.

Models

We evaluated two competing models of maternal investment. The first model represented our hypothesized bet-hedging strategy, in which timing of parturition was adjusted as a function of dam condition in spring (Fig. 2). The second model was a null model in which calf birth date was decoupled from dam body condition (Fig. 3). Both models consisted of a series of life stage-specific equations (both deterministic and stochastic) that linked hypothesized patterns of energy transfer and investment to patterns of demographic vital rates. Specifically, the models were individual based, and the energy transfer relationships were derived either from our own empirical data or from previously published data for elk (Tables 1 and 2). We initialized our models by randomly generating spring body condition values (% ingesta-free body fat) for 100 pregnant female elk from an empirical distribution derived from data collected at our study site (see *Simulations*). Model equations then linked this initial distribution of dam condition values to timing of parturition, birth mass of young, and maternal investment in gestation and lactation according to each respective strategy (i.e., null vs. bet-hedging). We tracked condition and survival of all modeled individuals until they either died or the model run ended. Each run consisted of 30 breeding seasons (years). Adult elk that survived through the following winter attempted to reproduce again; calves that survived the winter transitioned to the yearling stage, and yearlings that survived became adults.

Bet-hedging model

In the bet-hedging model (Fig. 2), initial condition of the dam determined the date of parturition, with cows in poorer condition giving birth later and investing concomitantly more energy in gestation (equations 1 and 4, Table 1). Calves born later were also larger (equation 2, Table 1) and were more likely to survive their first month of life (equations 3 and 12, Table 1). In contrast to gestation, date of birth was negatively related to investment in lactation (equation 5, Table 1), allowing cows that started the simulation in poor condition to accrue somatic energy reserves more rapidly during summer. Investment in lactation, however, was positively related to calf growth rate over summer (equation 6, Table 1), thereby influencing calf body mass at the onset of winter (equation 7, Table 1). Early-winter body mass of calves was positively related to overwinter survival probability (equation 8, Table 1). Notably, however, the strength of this empirically derived relationship was weaker than the relationship between birth mass and survival probability during the first month of life; this was a key component of the bet-hedging strategy. Because calf growth rates during summer were driven by maternal investment in lactation, they were negatively related to dam condition at the onset of winter (equations 9 and 10, Table 1). Dams in better condition in early winter had a higher overwinter survival probability (equation 11, Table 1). Both adults and calves that survived through winter contributed to reproductive performance and associated population growth in the following year (equations 13a and 13b, Table 1).

Null model

The primary difference between the null (Fig. 3) and the bet-hedging model was the decoupling of dam body condition from calf birth date in the null model. Accordingly, both dam condition and calf birth mass were generated from empirical distributions derived from field data collected at our study site (see *Simulations*). Because dams in the null model were not modulating timing of parturition (and thus calf birth mass and cost of gestation) based on spring body condition, energy devoted to lactation was determined by post-parturition body condition of the dam (equation 4, Table 2). Post-parturition condition of the dam was determined by subtracting energy devoted to gestation from spring body condition using a 37,000 kJ/kg of calf mass conversion (equation 3, Table 2). Calf mass in kg was divided by the mass of the cow (drawn from a normal distribution fit to empirical data from Starkey) to determine %IFBF lost due to investment in gestation, which was then subtracted from spring condition to determine post-parturition condition of the dam. Dams in better condition post parturition devoted more energy to lactation (equation 4, Table 2), thereby increasing calf growth rate during the summer (equation 5, Table 2). Faster growth rates resulted in larger body mass of calves at the onset of winter (equation 6, Table 2), increasing the probability of overwinter survival (equation 7, Table 2). Faster calf growth rates also reduced condition of the dam at the onset of winter (equations 8 and 9, Table 2), resulting in lower overwinter survival probability of the dam (equation 10, Table 2). As in the bet-hedging model, adults and calves that survived winter contributed to population productivity in the following year (equations 12a and 12b, Table 2).

Simulations

We used the R programming language (R Core Team, 2021, Version 4.1.0) to run the simulations for both models. We began each simulation with a starting population of 100 two-year-old female elk and ran the model for 30 calving seasons. At the beginning of each season, including the initial one, we assigned each cow a body condition value using a Weibull distribution ($k = 3.87$, $\lambda=6.15$) which was determined by fits to the Starkey data using the fitdist function from the fitdistrplus package (Delignette-Muller and Dutang 2015). Adult female elk were assigned an 85% probability of pregnancy each season, while yearlings were given a 10% probability, each with an equal probability of giving birth to a male or female calf (Long et al. 2014, 2016).

We tracked the fate of each individual elk throughout each 30-year model run (Fig. 4, 5 and 6), along with age, sex, age category (i.e., yearling or adult), energy devoted to lactation, and body condition in both the spring and early winter. Calf survival (through early summer and through winter), sex, date of birth, birth weight, growth rate, and early winter weight were tracked in association with each dam. Calves that survived the winter transitioned to the yearling stage class, and yearlings that survived the winter became adults. To simulate the effect of hunting on adult male mortality we used harvest data from Western Oregon compiled by Biederbeck et al. (2001). Male mortality from harvest was independent of overwinter mortality, and harvested males were removed from the population prior to the onset of winter. Other mortalities were subtracted from the population during the year in which they occurred, and overall annual mortality was tracked each year.

At the population level, the number of adult and yearling females and males, and the number of calves, were recorded each year. Mortality rates for each group were likewise recorded. In addition, the mean and variance of age, calf mass (birth and early winter), survival of each group (by sex and age category), adult body condition (spring and early winter), and winter severity were tracked annually. Lambda was recorded for each season and average lambda was recorded for each iteration. Summary statistics for all variables were recorded at the end of each 30-year iteration, and we ran 1,000 iterations of each model for each of 10 levels of winter severity (see below).

Winter severity

To simulate interannual variation in winter severity we used a modified version of Farnes' Index of Winter Severity (Farnes1996). We used SNOTEL data collected at Bowman Springs (a weather station located near Starkey with similar climate and topography) from December 1st through April 15th, 2006–2020. A 'severe' winter day was defined as a day in which the minimum temperature was below -18 °C, when additional food intake is needed to compensate for increased metabolic demands (Farnes 1991), and/or when snow depth was ≥46 cm, which greatly impedes the ability to forage and move about the landscape.

Using the fitdistrplus package (Delignette-Muller and Dutang, 2015) in R, we found that a beta distribution with $\alpha = 3$ and $\beta = 2.5$ best described the likelihood that a day would have severe conditions. Therefore, in each simulation we sampled randomly from this distribution and multiplied the resulting probability by the number of days of winter from (136 days from December 1st through mid-April 15th) to calculate the total number of severe days experienced by elk in each winter season. To simulate winters that were milder or more severe than those estimated from the SNOTEL data approximated interannual variation in weather patterns by altering α and β by increments of 0.25 in opposite directions. In doing so we altered the weight of the distribution so that the skew moves from left to right with each regime. Table 3 shows the average number of severe winter days resulting from each change in parameters. The number of severe winter days then influenced whether or not calves survived through the winter (Table 1, equation 8 for the bet-hedge model and Table 2, equation 7 for the null model). We stored the results for each winter weather regime separately.

Stochasticity

To better reflect natural variation in the drivers of ungulate population dynamics we incorporated stochasticity into each of the two models. We accomplished this by selecting parameters for several key equations in each model (equations 1, 2, 6 and 7 in the bet-hedging model and equations 4, 5, and 6 in the null model) from corresponding prediction intervals in each model iteration using the predict and simulate functions in base R (Fig 5). We integrated stochasticity into these equations to capture the high level of variability in the empirical data from Starkey. We sampled from the 95% predication interval of the linear equation to obtain the output. We did so because of the associated uncertainty associated with a predicted unknown future variable.

Data analysis

We compared the effects of each maternal investment strategy (i.e., the null and bet-hedging models) on population performance by using paired t-tests to test for differences in lambda, final population size, survival (calf and adult), calf body mass (birth and early winter), average age, and adult body condition (spring and early winter) between the two models. Cohen's d was used to calculate the effect size of the differences between the bet-hedging and null models using R package effsize (Torchiano, 2020).

Results

Population dynamics

For winter conditions recorded at Starkey during the time of data collection (i.e., 'standard winter conditions', regime #7, Table 3), the finite rate of population growth (lambda) was significantly greater under the bet-hedging model (mean lambda = 1.14; Table 4) than under the null model (mean lambda = 1.11; Table 6). Moreover, the effect size was large (Cohen's d = 1.11; Table 8) across all winter severity regimes (Fig. 8a). As winters became more severe, the mean value of lambda declined under both models and the difference between the bet-hedging and null models increased, whereas the effect size decreased (Fig. 8a, Table 8). Mean population size at year 30 assuming standard winter conditions was likewise significantly higher under the bet-hedging model (3,909 ± 147 animals; Table 4) than under the null model (2,189 ± 79 animals; Table 6), and the effect size was again large

(Cohen’s d = 0.90, Table 8). As winter severity increased the difference between the two models and the effect size decreased (Tables 8, Fig. 8b). The two models of maternal investment also led to different age structures after 30 years of population growth. Mean age of adult females in year 30 was significantly higher under the null model (6.21 ± 0.39 years; Table 6) than under the bet-hedging model (5.87 ± 0.37 years; Table 4) for the standard winter regime, and this difference increased as winters became more severe (Table 8, Fig. 8c). The effect size remained small for all 10 winter regimes (Cohen’s d=0.21 for the standard winter regime; Table 8).

Adult survival and body condition

Female survival was higher (Cohen’s d = 4.81, Table 9) for the bet-hedging (0.96±0.0006, Table 4) model than for the null model (0.95±0.0006, Table 6) under the standard winter regime. Female survival decreased, as did the effect size, under both models as winters became more severe (Table 9, Fig. 9a), but the difference in survival between models remained fairly constant. Male survival was equivalent between the bet-hedging (0.71±0.009; Table 4) and null models (0.71±0.008; Table 6) (Cohen’s d = 0.16; Table 9) for all winter regimes. Male survival for both models decreased with increasing winter severity (Fig. 9b). Mean early-winter body condition also was significantly higher under the bet-hedging model (7.65±0.03 % IFBF for the bet-hedging model vs 7.42±0.04 % IFBF for the null model; Tables 5 and 7) under the standard winter regime (Cohen’s d = 35.65; Table 9). The difference between the two models remained consistent across the range of winter severities we tested (Fig 9c), although the effect size declined with increasing winter severity.

Calf survival and body mass

There was no significant difference in summer calf survival between the two models for the standard winter regime (0.61±0.002 for the both the bet-hedging and null models; Cohen's d = 0.024; Tables 5,7, and 10), and this result was consistent across the range of winter severities we tested (Fig. 8a). In contrast, calves in the bet-hedging model had a significantly higher rate of winter survival (0.59 ± 0.02, Tables 5 and 10, Fig. 10b) than calves in the null model (0.54 ± 0.02, Table 7) (Cohen's d = 0.58; Table 10). This result was driven by lower mean body mass of calves at the onset of winter under the null model (97.10 ± 0.9 kg for the null model versus 99.98 ± 0.6 kg for the bet-hedging model; Tables 5, 7, and 10; Cohen's d = 14.62), and was unaffected by changing winter severity (Fig. 10c).

Discussion

Results from our simulations support our prediction that elk populations employing a state-dependent bet-hedging strategy of maternal investment would increase at a faster rate than populations in which timing of parturition was independent of dam condition in spring. The higher average lambda predicted under the bet-hedging model was driven by (1) more calves surviving through winter due to a larger average body mass at the onset of winter, and (2) higher overwinter survival of females stemming from increased early-winter body condition. Interestingly however, the impact of higher early-winter winter body mass on overwinter calf survival decreased as winters became more severe, making female survival more important to population performance under harsher winter conditions. Females that delayed parturition and gave birth to larger calves subsequently invested less energy in lactation and entered winter in better condition, improving their probability of survival. The importance of female elk favoring investment in their own survival over investment in their offspring can be seen in the changing age structure of the population. As winters became more severe, the average age of females in the population increased because fewer calves were recruited into the breeding population. This buffering of the population against temporal variation in recruitment by adult females has been demonstrated in wild populations of elk, caribou, moose, and other ungulates (Gaillard et al. 1998). By selectively investing in their own body condition rather than on offspring (those offspring being more likely to die when times are lean), females can live to reproduce another year when times are better.

One surprising result of our analyses was the similarity in average birth mass between the bet-hedging and null models, despite birth mass being derived from two stochastic equations in the bet-hedging model and from an empirically derived normal distribution in the null model. This result implies that the methods used to generate birth mass in the bet-hedging model are reliable and produced realistic estimates of calf birth mass. In addition, because both models produced a similar range of birth masses, the differences in early-winter calf mass and overwinter survival of calves between the two models stemmed from the reduced overall (i.e., over the course of the summer) cost of delaying parturition. Cows give birth to larger calves while reducing lactation costs to maximize their own body condition. Many species of capital breeding ungulates such as white-tailed deer (Simard, et al., 2014), caribou (Post, et al., 2003) and red deer (Clements, et al., 2011) can adjust their gestation based on environmental and physiological cues, providing support for the hypothesis that such species can delay parturition to facilitate better allocation of resources and improve the survival of the dam and offspring.

While in the absence of other limiting factors elk populations using the hypothesized bet-hedging strategy outperformed populations using the null strategy due to more effective allocation of resources by the dam to both herself and her offspring, the bet-hedging model makes several non-trivial assumptions. First, the model assumes that predation, nutrition, or other factors do not lead to synchronous parturition among females and that adjustment of gestation length is not functionally possible. In systems where green-up occurs rapidly during a brief window, such as the arctic (Post et al. 2003), females may not have the luxury of delaying parturition. Likewise, intense predation pressure may necessitate birthing pulses to saturate predators with more offspring than can be consumed (Post et al. 2003). These conditions would likely reduce or eliminate the advantages of maternal bet-hedging. Second, the bet-hedging model assumes that the simulated animals are true capital breeders, using stored energy reserves to 'fund' both gestation and lactation, and therefore that the nutritional landscape has no overt effect on condition and survival of either the calf or the dam. In contrast, income breeders, such as many African ungulates (Ogutu et al. 2014), are dependent upon plant phenology and the availability of high-quality forage for successful reproduction. Most ungulate species likely fall somewhere between these two extremes (e.g., Noyes et al. 2002), but the closer to the income end of the continuum a species falls, the less advantageous the bet-hedging strategy is likely to be. An additional consequence of the capital breeding assumption is that the simulated female elk in both models are given an allotment of energy that is then divided among gestation, lactation, and somatic reserves. For the bet-hedging model, energy devoted for lactation is determined by a linear model regressing lactation on the energy devoted to gestation. For the null mode energy devoted to lactation was regressed on the female's post-parturition body condition. This gives the bet-hedging model an inherent advantage due to the linear equation used in the null model having a steeper slope, and thus incurring a higher cost, for lactation. If the influence of date of parturition on overall time spent nursing was included in the null model, then simulated calves in that model might be larger at the onset of winter and thus have a higher probability of survival. We plan to evaluate this possibility in later simulations. A third assumption of our analyses is that in both models, summer calf mortality was assumed to be driven by predation during the first month of life, which is often the case in large ungulates. However, predation can influence population dynamics throughout the year, especially when forage is sparse and large predators are common (Parker et al. 2009, Ogutu, et al. 2014). But for the purposes of our model and the system being simulated it has no bearing on our conclusions. If we wanted to model a species that experienced more constant predation pressures, say those of the African savannah, then we would need to take this into account. Population density also was not taken into account in either of our models. Most vital rates of ungulates like elk are subject to density dependence (Singer et al. 1997). Again though, there is no reason to believe that such effects would manifest differently between our two models, and thus our general conclusions are likely unaffected by the lack of density dependence. Finally, our models assumed that calf survival, but not adult survival, was directly affected by winter severity. For the most part adult elk survival is not affected by winter severity (Singer et al. 1997), although under certain conditions, such as at high density or during extreme environmental events (such as forest fires) severe winters can increase adult winter mortality (Taper and Gogan 2002). Accordingly, this assumption seems reasonable in our models.

Ungulates have been shown to adjust gestation length in response to environmental and physiological cues (Clements et al. 2011), and the results of our modeling support the hypothesis that a state-dependent version of this tactic can improve population performance. When female elk in our bet-hedging model delayed parturition based on poor nutritional condition in spring, both they and their offspring experience a higher probability of survival to the following year. This result was consistent across a range of winter severities and could indicate that large ungulates like elk can buffer themselves against the extreme climatic variation produced by favoring somatic growth over the survival of offspring (Hansen et al. 2019). Future empirical work should aim to test the predictions of our model, including comparisons of parturition and survival data from longitudinal studies within and among species. The knowledge gained from this and future studies will help better understand the evolution of life-history strategies and how they influence patterns of population performanc

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Tables and Figures

Figure 1: The location of our study area, the Starkey Experimental Forest and Range, Oregon, U.S.A.

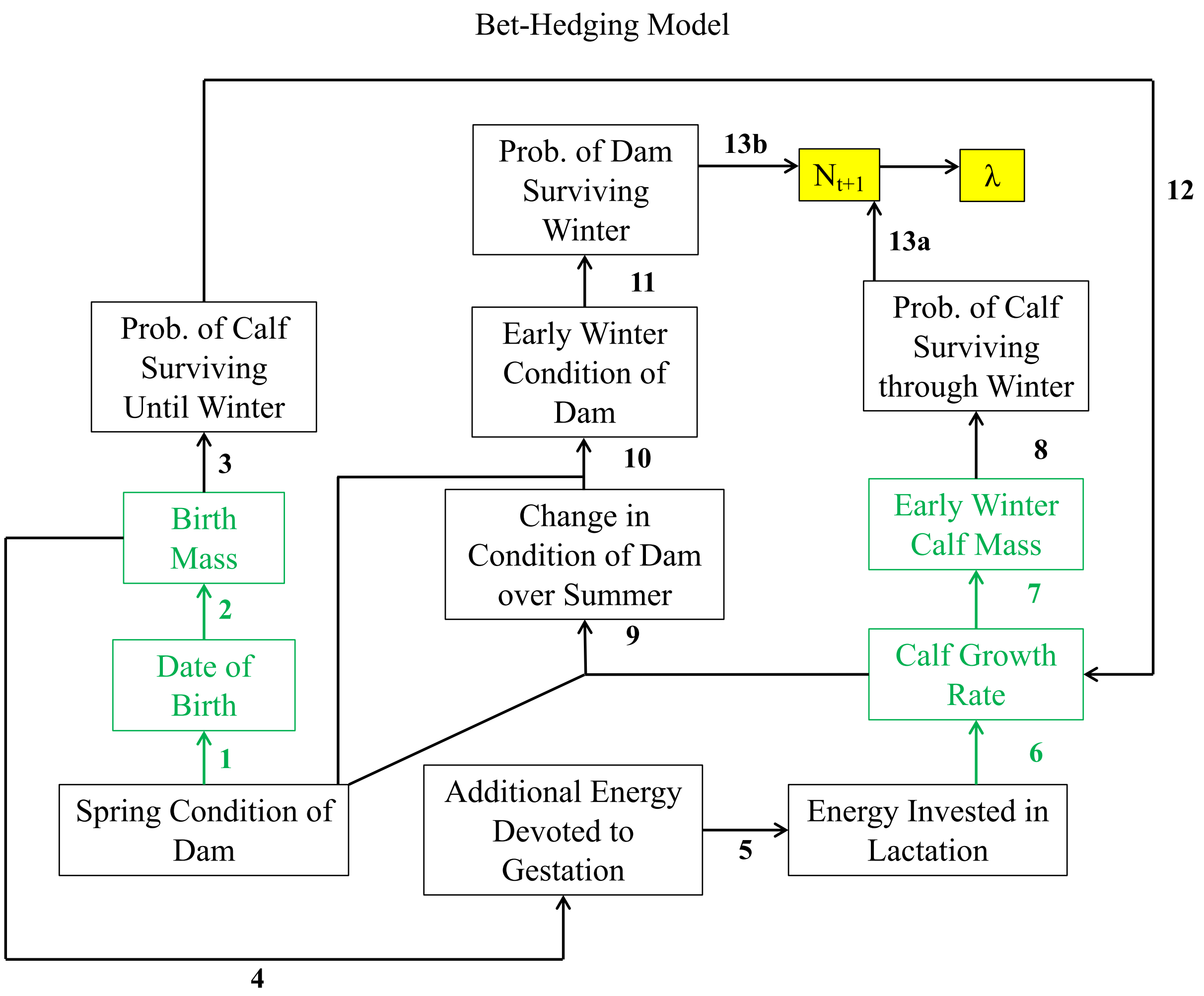


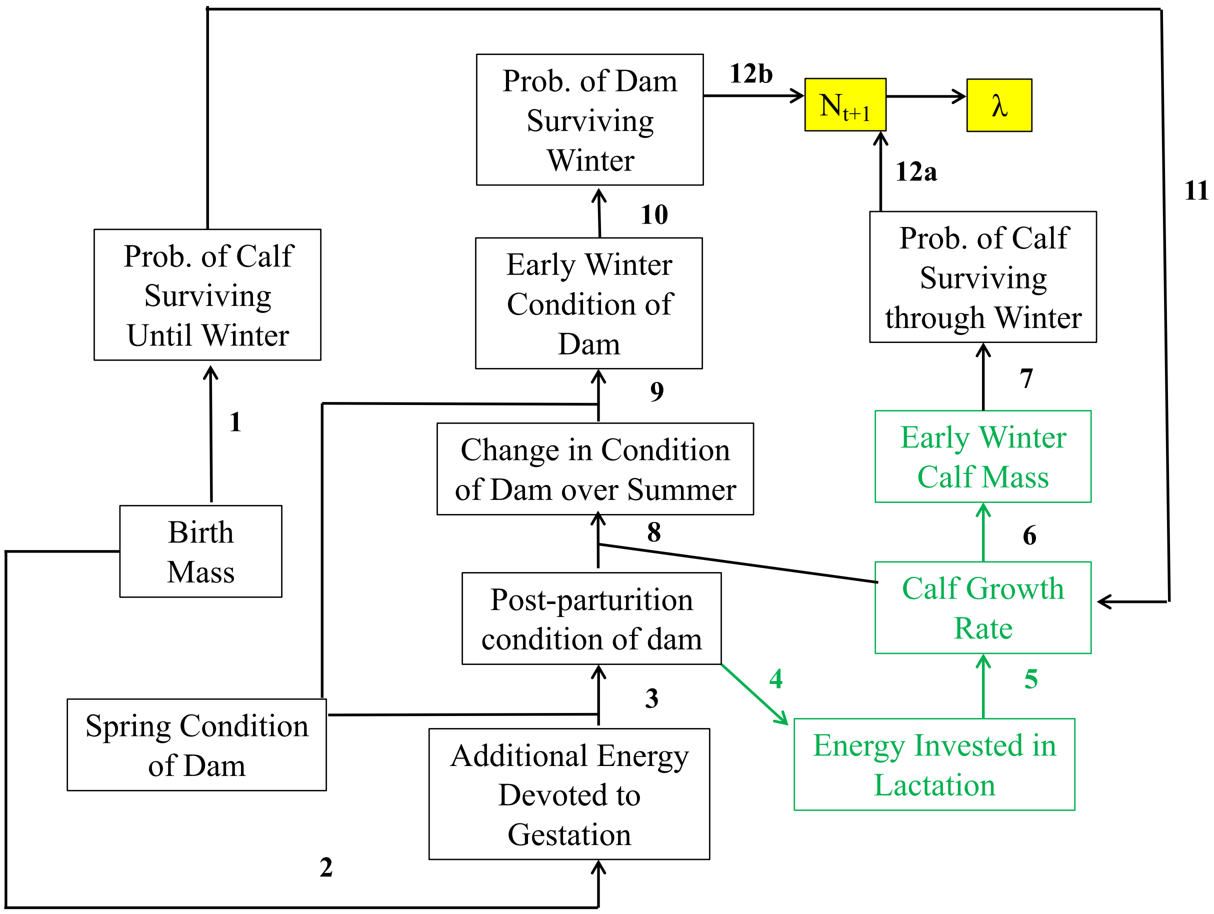
Figure 2: Graphical representation of the maternal bet-hedging model. Numbers reference equations (described in detail in **Table 1**) that link model variables enclosed in boxes. Green numbers/boxes indicate stochastic equations whereas black numbers/boxes indicate deterministic equations. The model was initialized by assigning spring condition values (% ingesta-free body fat) to 100 adult female elk at random from the empirical distribution of condition data obtained at our study site.

Table 1

Equation	Data generated	Formula	Output units	Source
1	Calf birthdate	-2.485 × Spring Condition + 163.11	Julian day	Starkey data
2	Birth mass	0.128 × Julian DOB – 2.145	Mass in Kg	Starkey data
3	Prob. of Calf Surviving Until Winter	-0.0101 x (Birth Mass)^2 + 0.4127 x Birth Mass – 3.2477 (females) -0.0016 x (Birth Mass)^3 + 0.0823 x (Birth Mass)^2 – 1.2594 x Birth Mass + 6.048 (males)	Survival probability	Starkey data
4	Additional Energy Devoted to Gestation	(Birth Mass – Minimum Birth Mass) × 12,937 kJ/kg	Kilojoules	Hudson et al. 2002
5	Energy Invested in Lactation	-5.552 × Additional Energy for Gestation + 3,000,000	Kilojoules	Starkey data
6	Calf Growth Rate	1×10^{-7} × Energy Invested in Lactation + 0.117	Kilojoules	Starkey data
7	Early Winter Calf Mass	193.13 kJ/kg × Calf Growth Rate + 25.398	Mass in Kg	Starkey data
8	Probability of Calf Surviving through Winter	-0.0120088 x (Early Winter Calf Mass)^2 + 3.1656 x Early Winter Calf Mass – 109.9	Survival probability	Cook et al. 2004
9	Change in Condition of Dam over Summer	(-0.7 × Spring Condition) – (6.297 × Calf Growth Rate) + 8.423	Percent ingesta-free body fat	Starkey data

10	Early Winter Condition of Dam	Spring Condition + Change in Condition	Percentage ingesta-free body fat	Starkey data
11	Probability of Adults Surviving through Winter	(exp(-4.717 + 0.955 x Winter Condition))/(1+exp(-4.717 + 0.955 x Winter Condition))	Survival probability	Cook et al. 2004
12	Calves Surviving to Early Winter	Individual calves that survive until winter will be fed into the early winter calf mass and subsequent overwinter survival equations	NA	NA
13a and 13b	Lambda	N_{t+1}/N_t	Population growth rate	NA

Table 1: Equations and associated data sources used to parameterize the maternal bet-hedging model. Equation numbers correspond to the numbering in **Fig. 2**. Green text indicates equations in which the results are stochastic due to being simulated using a prediction interval.



Null Model

Figure 3: Graphical representation of the null model of maternal investment. Numbers reference equations (described in detail in **Table 2**) that link model variables enclosed in boxes. Green numbers/boxes indicate stochastic equations whereas black numbers/boxes indicate deterministic equations. The model was initialized by assigning spring condition values (% ingesta-free body fat) to 100 adult female elk at random from the empirical distribution of condition data obtained at our study site.

Table 2

Equation	Data generated	Formula	Output	Source
1	Prob. of Calf Surviving Until Winter	-0.0101 x (Birth Mass)^2 + 0.4127 x Birth Mass – 3.2477 (females) -0.0016 x (Birth Mass)^3 + 0.0823 x (Birth Mass)^2 – 1.2594 x Birth Mass + 6.048 (males)	Survival probability	Starkey data
2	Additional Energy Devoted to Gestation	(Birth Mass – Minimum Birth Mass) × 12,937 kJ/kg	Kilojoules	Hudson, et al. 2002
3	Post-parturition condition of dam	Spring condition-(((Gestation Energy/37,000 kJ/kg)/Body mass * 100)	Percentage ingesta-free body fat	Starkey data
4	Energy Invested in Lactation	113,327× Post-parturition Condition + 1820318	Kilojoules	Starkey data
5	Calf Growth Rate	1×10^{-7} × Energy Invested in Lactation + 0.117	Kilojoules	Starkey data
6	Early Winter Calf Mass	193.13 kJ/kg × Calf Growth Rate + 25.398	Mass in Kg	Starkey data
7	Probability of Calf Surviving through Winter	-0.0120088 x (Early Winter Calf Mass)^2 + 3.1656 x Early Winter Calf Mass – 109.9	Survival probability	Cook, et al. 2004
8	Change in Condition of Dam over Summer	(-0.7 × Spring Condition) – (6.297 × Calf Growth Rate) + 8.423	Percentage ingesta-free body fat.	Starkey data.

9	Early Winter Condition of Dam	Post-parturition condition + Change in Condition	Percentage ingesta-free body fat	Starkey data
10	Probability of Adults Surviving through Winter	(exp(-4.717 + 0.955 x Winter Condition))/(1+exp(-4.717 + 0.955 x Winter Condition))	Survival probability	Cook, et al. 2004
11	Calves Surviving to Early Winter	Individual calves that survive until winter will be fed into the early winter calf mass and subsequent overwinter survival equations	NA	NA
12a and 12b	Lambda	N_{t+1}/N_t	Population growth rate	NA

Table 2: List of the equations that generate the data for the Null model. Equation numbers match the numbering in **Fig. 3**. Green text indicates equations in which the results are stochastic due to being simulated using a prediction interval.

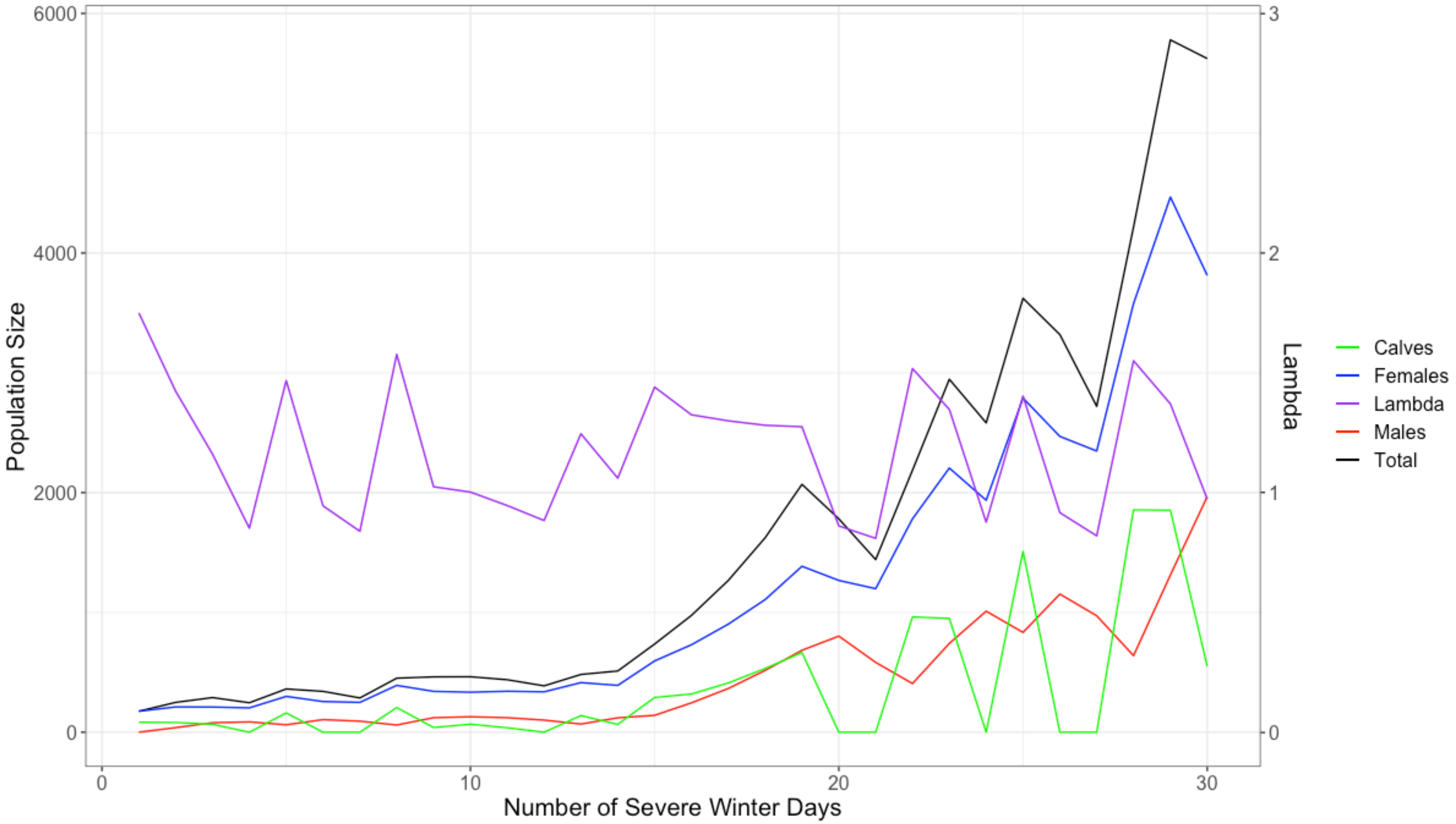


Figure 4: Patterns of population growth for a simulated elk population over a 30-year time period extracted from a single iteration of the maternal bet-hedging model during a standard winter (with an average of approximately 70 severe winter days). Blue, green, and red lines represent females, males, and calves respectively, and the black line shows total population growth. The finite rate of population increases each year, lambda, is shown in purple.

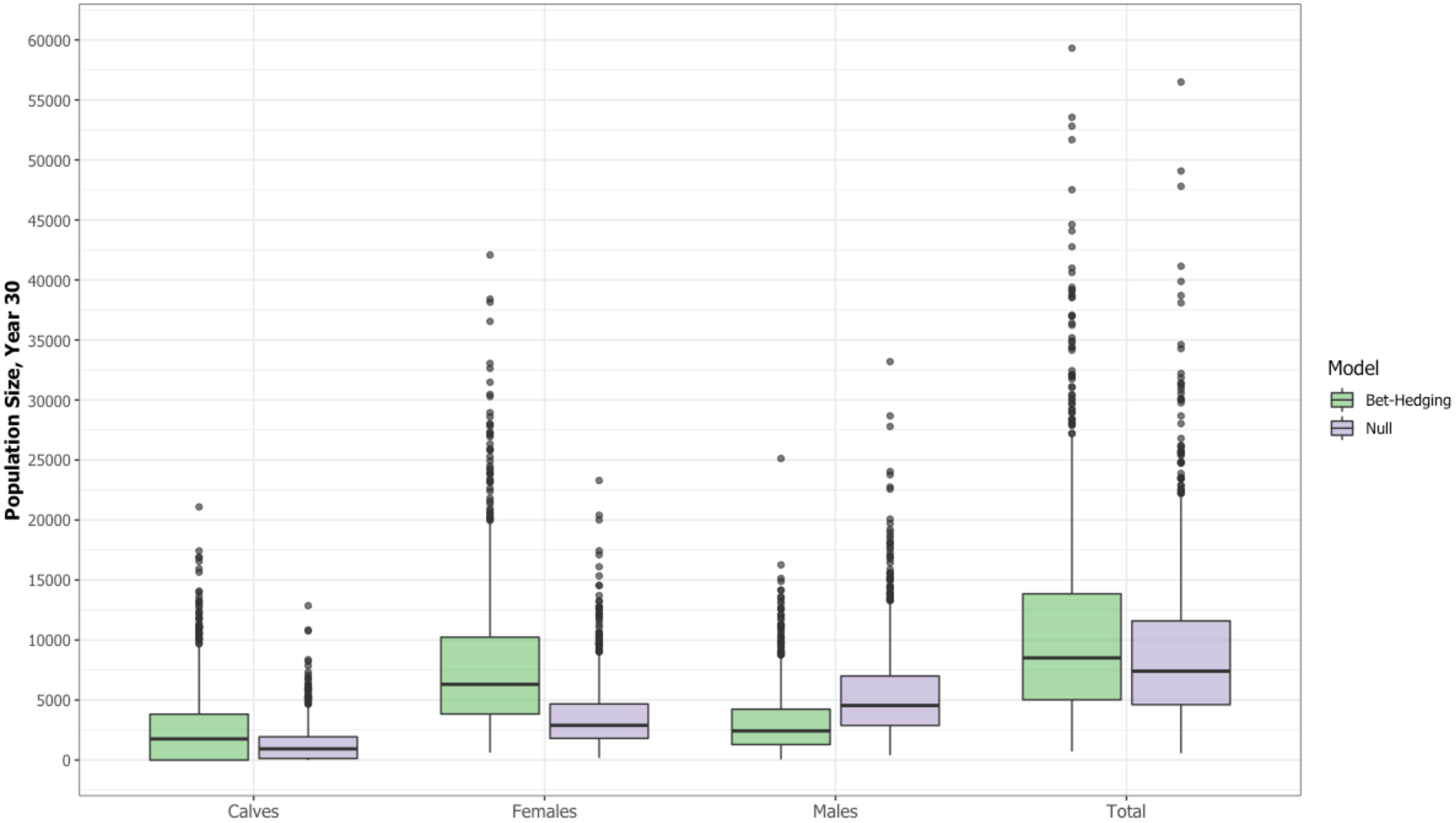


Figure 5: Distribution of population output for the bet-hedging (green) and null (purple) models over 1000 iterations using the standard Starkey winter severity (Beta~(3,2.25), mean number of severe winter days=69.5). Data are the number of animals (calves, females, males, and total population), at the final year of iteration (year 30).

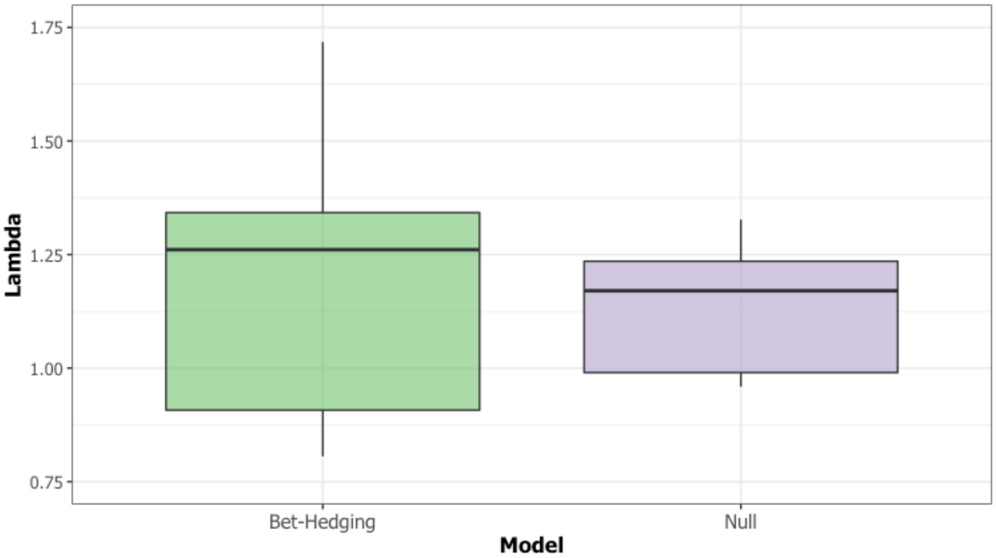


Figure 6: Distribution of lambda for population for the bet-hedging (green) and null (purple) models over 1000 iterations using the standard Starkey winter severity (Beta~(3,2.25), mean number of severe winter days=69.5). Data are for the final year of iteration (year 30).

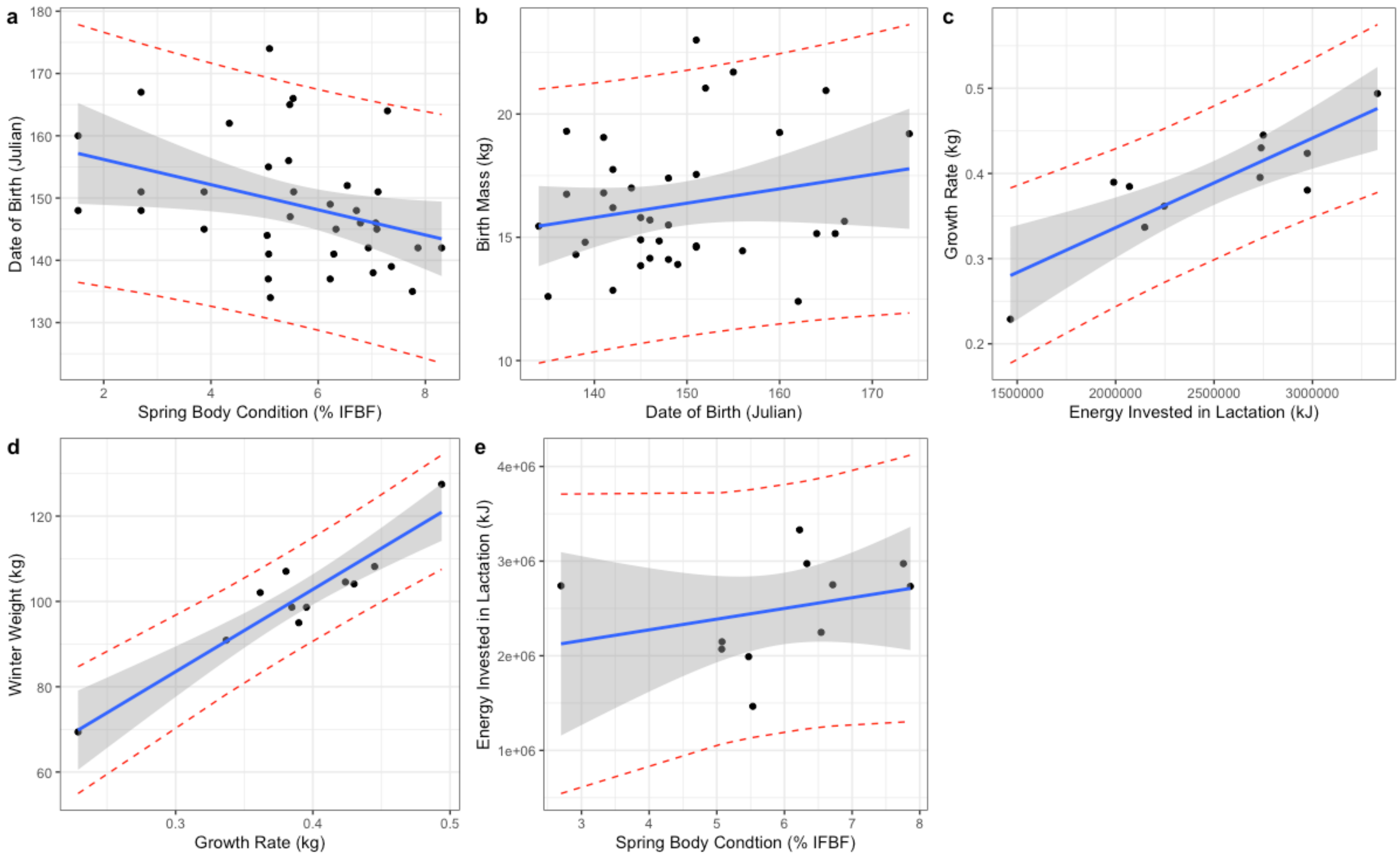


Figure 7: Empirical relationships between (a) dam body condition (percent ingesta-free body fat) in spring and date of birth, (b) date of birth and calf birth mass, (c) energy invested in lactation and calf growth rate, (d) calf growth rate and calf winter mass, and (d) dam body condition in spring and energy invested in lactation. Relationships illustrated in panels a, b, c, and d were used to parameterize the bet-hedging model, whereas only relationships illustrated in panels c, d, and e were used in the null model. The blue line is the line of best fit and corresponds to the equations in Figs. 2 and 3 (equations 1, 2, 6 and 7 in the bet-hedging model and equations 4, 5, 6 in the null model). Dotted red lines show the prediction intervals used to integrate stochasticity into the simulations, while shaded grey areas show 95% confidence intervals for reference

Table 3

Regime #	α	β	Number of Severe days	Standard Deviation
1	1.5	3.75	34.59	5.88
2	1.75	3.5	40.70	6.38
3	2	3.25	46.42	6.81
4	2.25	3	52.33	7.23
5	2.5	2.75	58.18	7.63
6	2.75	2.5	64.03	8.00
7	3	2.25	69.50	8.34
8	3.25	2	75.50	8.69
9	3.5	1.75	81.46	9.03
10	3.75	1.5	87.32	9.34

Table 3: Alpha and beta parameter values for beta distributions used to determine the number of severe winter days in a given season. The average and standard deviation of the number of severe winter days after 1,000 model iterations are presented for each of 10 winter severity regimes ranging from mild (regime #1) to severe (regime #10). The red highlighted distribution (Regime #7) reflects the current weather conditions at Starkey.

Table 4

Mean # Severe Winter Days	Population, Year 30		Lambda		Age, Year 30		Female Survival		Male Survival	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
34.59	36,158.3	7,681.79	1.22	0.08	4.18	3.99	0.96	0.009	0.74	0.07
40.7	30,394.9	7,852.48	1.21	0.10	4.29	4.11	0.96	0.009	0.74	0.07
46.42	23,517.9	7,679.78	1.20	0.11	4.43	4.29	0.96	0.009	0.73	0.08
52.33	17,426.2	6,870.92	1.19	0.13	4.61	4.52	0.96	0.009	0.73	0.09
58.18	11,275.3	5,422.25	1.18	0.15	4.91	4.90	0.96	0.010	0.72	0.11
64.03	7,053.83	3,719.17	1.16	0.16	5.25	5.31	0.96	0.011	0.72	0.12
69.5	3,909.23	2,377.38	1.14	0.17	5.87	6.00	0.96	0.012	0.71	0.14
75.5	2,039.44	1,328.45	1.11	0.18	6.65	6.83	0.96	0.013	0.70	0.16
81.46	968.00	643.44	1.09	0.19	7.95	7.91	0.96	0.014	0.69	0.18
87.32	458.45	313.00	1.06	0.18	9.77	9.10	0.96	0.016	0.67	0.21

Table 4: Means and standard deviations (*SD*) of output from the bet-hedging model for each winter severity regime. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey.

Table 5

Mean # Severe Winter Days	**Adult Female Spring Body Condition**		**Adult Female Early Winter Body Condition**		**Calf Summer Survival**		**Calf Winter Survival**		**Calf Birth Mass**		**Calf Early Winter Mass**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
34.59	5.56	1.61	7.65	0.54	0.61	0.03	0.95	0.19	16.33	2.68	99.99	9.55
40.70	5.56	1.61	7.65	0.54	0.61	0.03	0.92	0.24	16.33	2.68	99.98	9.55
46.42	5.56	1.61	7.65	0.54	0.61	0.03	0.87	0.29	16.33	2.68	99.98	9.55
52.33	5.56	1.61	7.65	0.54	0.61	0.03	0.82	0.33	16.33	2.68	99.99	9.55
58.18	5.56	1.61	7.65	0.54	0.61	0.03	0.75	0.38	16.33	2.68	99.99	9.55
64.03	5.56	1.61	7.65	0.54	0.61	0.03	0.67	0.41	16.33	2.68	99.99	9.55
69.50	5.56	1.61	7.65	0.54	0.61	0.03	0.59	0.44	16.33	2.68	99.98	9.55
75.50	5.56	1.61	7.65	0.54	0.61	0.03	0.49	0.44	16.33	2.68	99.99	9.55
81.46	5.56	1.61	7.65	0.54	0.61	0.04	0.40	0.44	16.33	2.68	99.99	9.54
87.32	5.56	1.61	7.65	0.54	0.61	0.04	0.30	0.41	16.33	2.68	99.98	9.55

Table 5: Means and standard deviations (*SD*) of additional output from the bet-hedging model for each winter severity regime. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey.

Table 6

Mean # Severe Winter Days	Population, Year 30		Lambda		Age, Year 30		Female Survival		Male Survival	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
34.59	25,197.4	5,602.94	1.20	0.08	4.22	4.03	0.95	0.01	0.74	0.07
40.70	20,288.7	5,744.80	1.20	0.09	4.33	4.17	0.95	0.01	0.73	0.08
46.42	15,027.4	5,032.88	1.18	0.11	4.53	4.39	0.95	0.01	0.73	0.08
52.33	10,618.8	4,333.49	1.17	0.12	4.75	4.67	0.95	0.01	0.73	0.09
58.18	6,624.33	3,027.32	1.15	0.14	5.13	5.08	0.95	0.01	0.72	0.11
64.03	3,941.16	2,039.86	1.14	0.15	5.54	5.60	0.95	0.01	0.72	0.12
69.50	2,189.32	1,280.69	1.11	0.16	6.21	6.29	0.95	0.01	0.71	0.13
75.50	1,106.46	712.08	1.09	0.17	7.21	7.21	0.95	0.02	0.70	0.15
81.46	560.84	347.08	1.07	0.17	8.45	8.27	0.95	0.02	0.69	0.18
87.32	266.30	174.91	1.04	0.17	10.53	9.47	0.95	0.02	0.68	0.22

Table 6: Means and standard deviations (*SD*) of output from the null model for each winter severity regime. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey.

Table 7

Mean # Severe Winter Days	**Adult Female Spring Body Condition**		**Adult Female Early Winter Body Condition**		**Calf Summer Survival**		**Calf Winter Survival**		**Calf Birth Mass**		**Calf Early Winter Mass**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
34.59	5.56	1.61	7.42	0.58	0.61	0.03	0.92	0.19	16.33	2.64	97.10	14.83
40.70	5.56	1.61	7.42	0.58	0.61	0.03	0.88	0.24	16.33	2.64	97.10	14.83
46.42	5.56	1.61	7.42	0.58	0.61	0.03	0.83	0.28	16.33	2.64	97.09	14.83
52.33	5.56	1.61	7.42	0.58	0.61	0.03	0.78	0.33	16.32	2.64	97.10	14.84
58.18	5.56	1.61	7.42	0.58	0.61	0.03	0.70	0.36	16.33	2.64	97.10	14.83
64.03	5.56	1.61	7.42	0.58	0.61	0.03	0.62	0.39	16.33	2.64	97.09	14.83
69.50	5.56	1.61	7.42	0.58	0.61	0.03	0.54	0.40	16.33	2.64	97.10	14.83
75.50	5.56	1.61	7.42	0.58	0.61	0.04	0.45	0.41	16.33	2.64	97.11	14.83
81.46	5.56	1.61	7.42	0.58	0.61	0.04	0.36	0.39	16.32	2.64	97.10	14.84
87.32	5.56	1.61	7.42	0.58	0.61	0.05	0.27	0.37	16.33	2.64	97.08	14.84

Table 7: Means and standard deviations (*SD*) of additional output from the null model for each winter severity regime. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey.

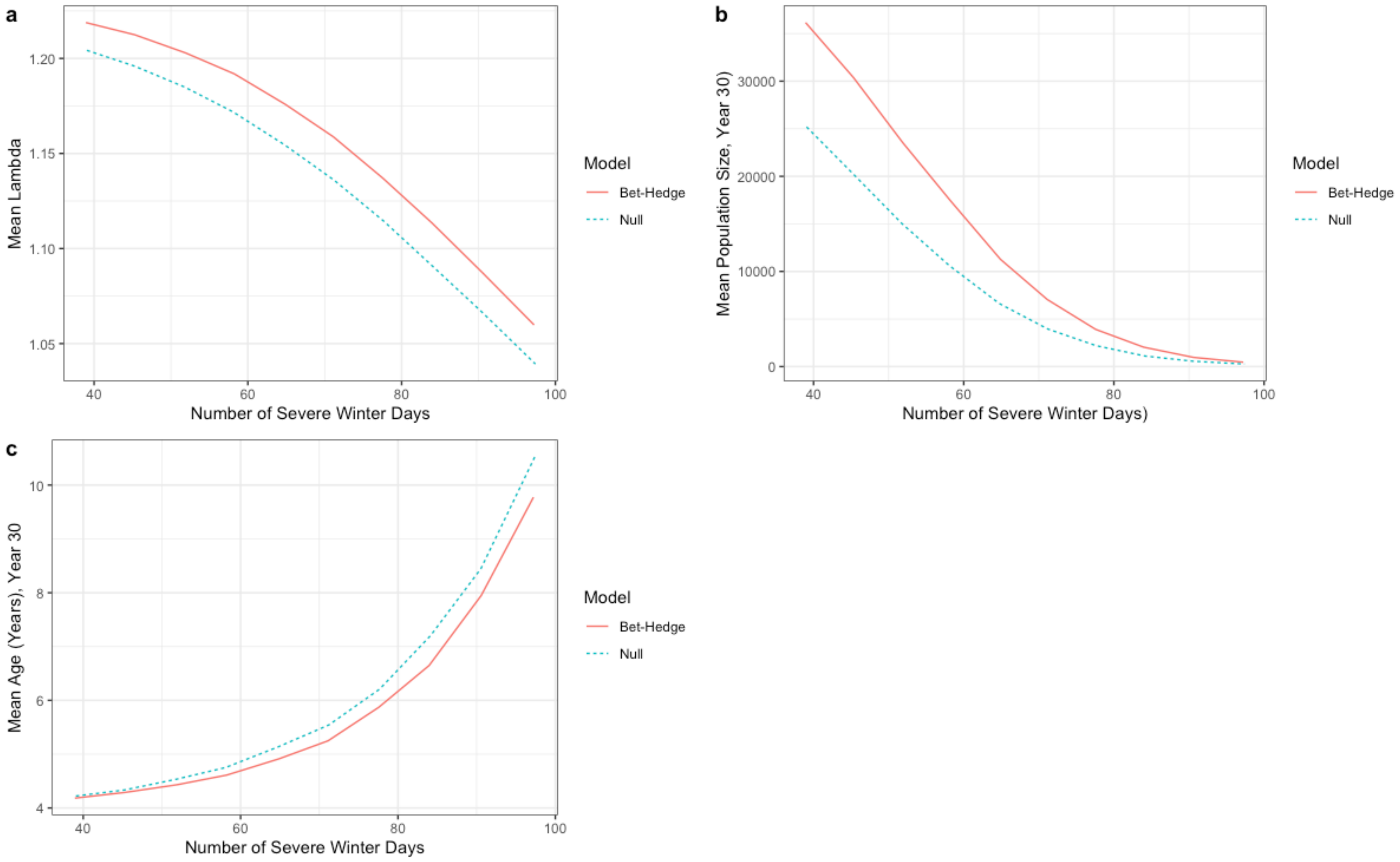


Figure 8: Relationships between (a) mean number of severe winter days and mean lambda, (b) mean population size at year 30, and (c) mean age at year 30 for the bet-hedging (red) and null models (blue).

Table 8

Average # Severe Winter Days	Mean Lambda		Mean Population Size, Year 30		Mean Age, Year 30	
	Difference	Cohen's d	Difference	Cohen's d	Difference	Cohen's d
34.59	-0.015***	1.80	-10,960.94***	1.63	0.04**	0.16
40.70	-0.016***	1.65	-10,106.21***	1.47	0.05**	0.13
46.42	-0.018***	1.48	-8,490.43***	1.31	0.10***	0.21
52.33	-0.020***	1.40	-6,807.40***	1.19	0.17***	0.28
58.18	-0.021***	1.29	-4,650.93***	1.06	0.22***	0.27
64.03	-0.023***	1.27	-3,112.67***	1.04	0.32***	0.32
69.50	-0.023***	1.11	-1,719.91***	0.90	0.29***	0.21
75.50	-0.023***	1.09	-932.98***	0.88	0.55***	0.31
81.46	-0.021***	0.96	-407.16***	0.79	0.50***	0.22
87.32	-0.021***	0.93	-192.15***	0.76	0.67***	0.21

Table 8: Differences in mean lambda, population size, and age at year 30, and associated effect size (using Cohen's D) between the bet-hedging and null models of maternal investment. Rows represent each of ten winter severity regimes by average number of severe winter days. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey. * P≤0.05, ** P≤0.001, *** P≥0.00001.

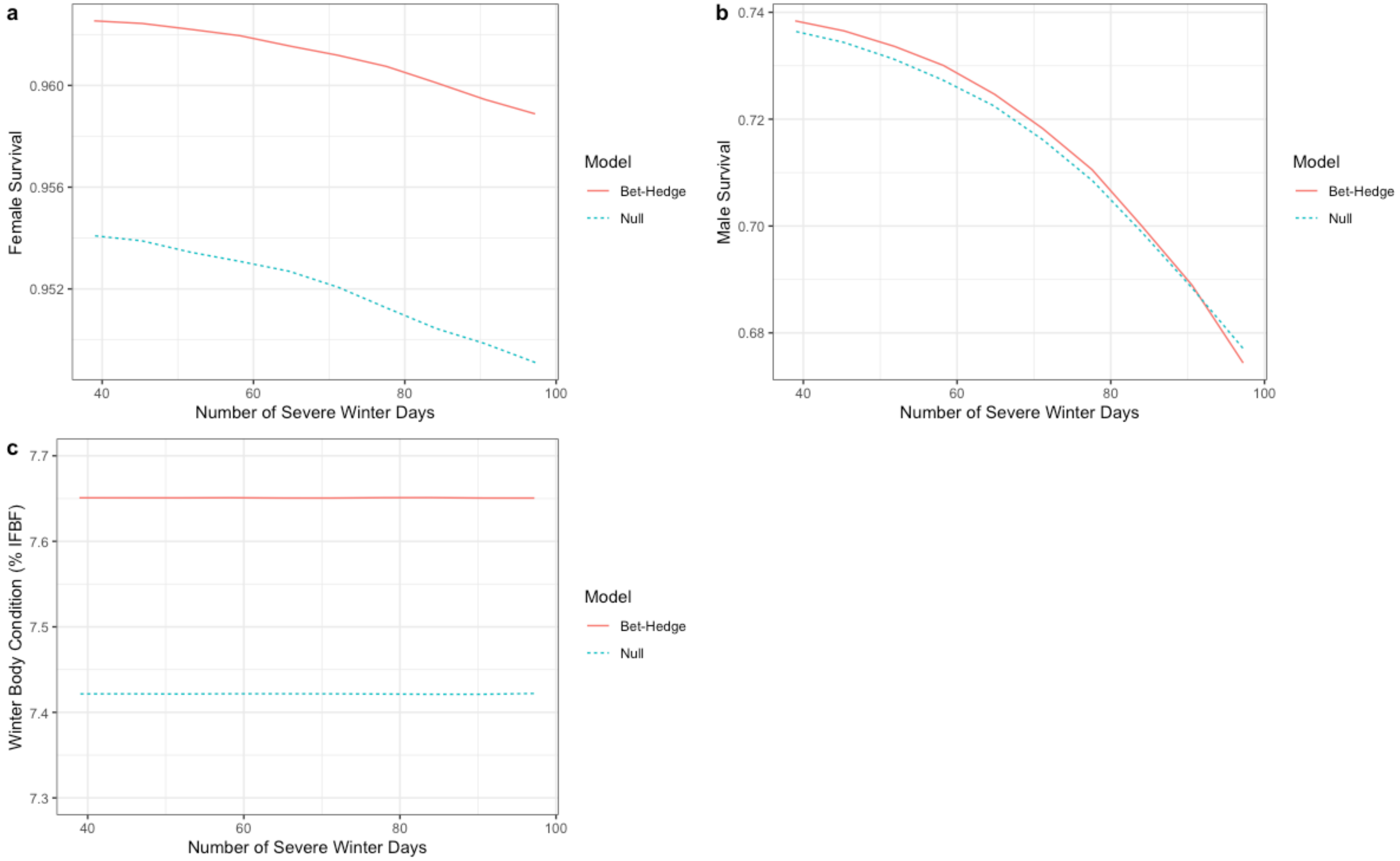


Figure 9: Relationships between (a) mean number of severe winter days and mean female survival, (b) mean male survival, and (c) mean early winter body condition for both the bet-hedging (red) and null models (blue).

Table 9

Mean # Severe Winter Days	Mean Female Survival		Mean Male Survival		Mean Early Winter Body Condition	
	Difference	Cohen's d	Difference	Cohen's d	Difference	Cohen's d
34.89	-0.008***	6.36	-0.002***	0.41	-0.23***	88.72
40.45	-0.009***	6.52	-0.002***	0.39	-0.23***	80.84
46.42	-0.009***	6.28	-0.002***	0.36	-0.23***	70.81
52.10	-0.009***	5.81	-0.003***	0.36	-0.23***	62.18
58.17	-0.009***	5.40	-0.002***	0.24	-0.23***	53.17
63.82	-0.009***	4.97	-0.002***	0.21	-0.23***	42.50
69.72	-0.010***	4.81	-0.002**	0.16	-0.23***	35.65
75.43	-0.010***	4.12	-0.001*	0.09	-0.23***	29.19
81.38	-0.010***	3.51	0.000	0.02	-0.23***	23.18
87.09	-0.010***	3.04	0.002*	0.08	-0.23***	19.11

Table 9: Difference between means and associated effect sizes (using Cohen's D) between the bet-hedge and null model for average adult survival, average female survival, average male survival and average early winter body condition. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey. * P≤0.05, ** P≤0.001, *** P≥0.00001.

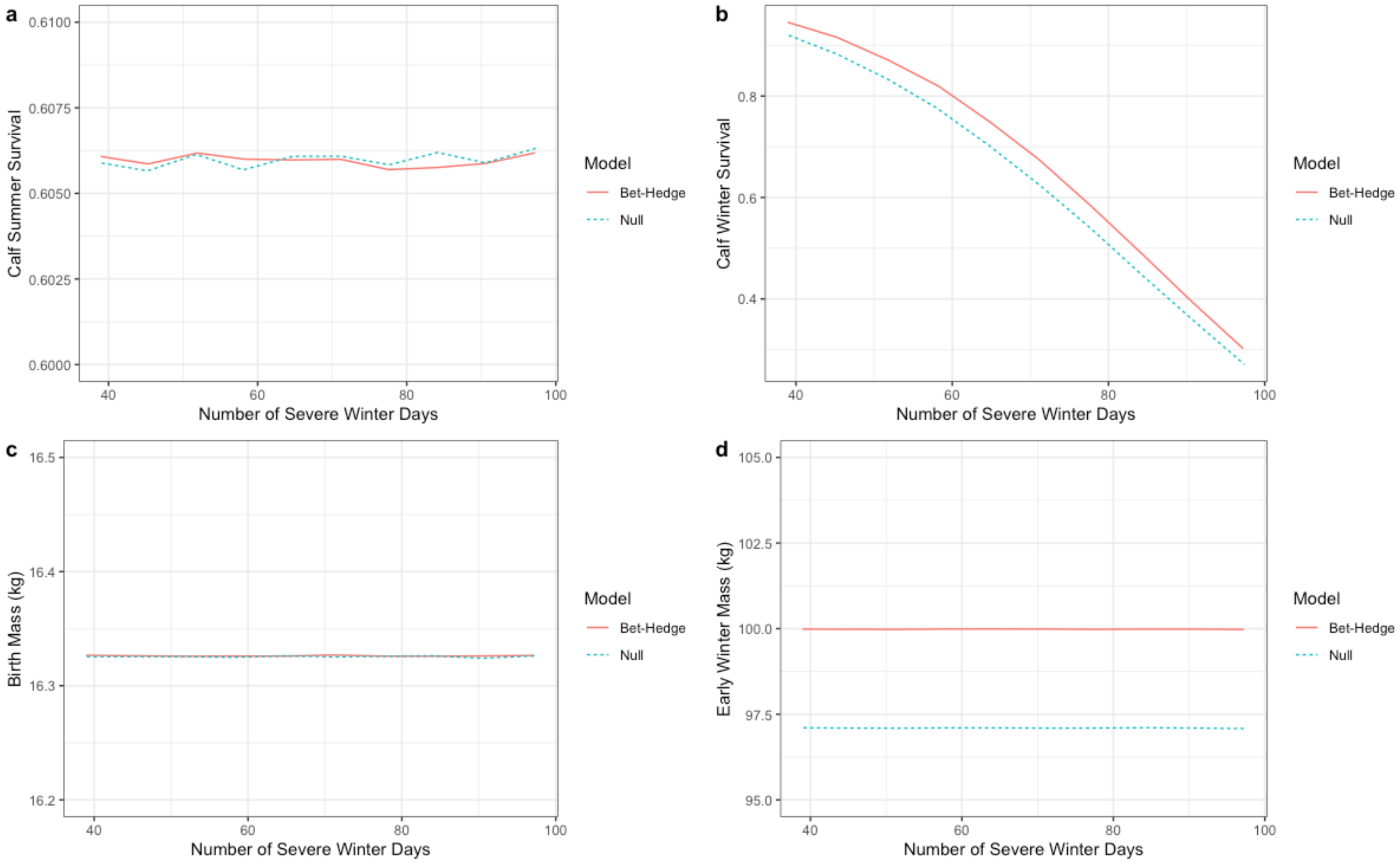


Figure 10: Relationships between (a) mean number of severe winter days and mean early calf survival, (b) mean winter calf survival, (c) mean calf birth mass, and (d) mean calf early winter mass for both the bet-hedging (red) and null models (blue).

Table 10

Mean # Severe Winter Days	Mean Calf Summer Survival		Mean Calf Winter Survival		Mean Calf Birth Mass		Mean Calf Early Winter Mass	
	Difference	Cohen's d	Difference	Cohen's d	Difference	Cohen's d	Difference	Cohen's d
34.89	-0.00019	0.040	-0.026***	0.73	-0.0012	0.130	-2.88***	18.66
40.45	-0.00020	0.042	-0.033***	0.76	-0.0008	0.072	-2.89***	18.73
46.42	-0.00004	0.009	-0.037***	0.72	-0.0003	0.026	-2.89***	17.81
52.10	-0.00031	0.063	-0.044***	0.72	-0.0009	0.068	-2.89***	16.88
58.17	0.00011	0.020	-0.046***	0.67	0.0002	0.012	-2.89***	16.54
63.82	0.00009	0.016	-0.050***	0.69	-0.0017	0.087	-2.90***	15.58
69.72	0.00014	0.024	-0.046***	0.58	-0.0001	0.004	-2.88***	14.62
75.43	0.00044	0.066	-0.045***	0.58	0.0003	0.010	-2.88***	13.09
81.38	0.00002	0.002	-0.034***	0.45	-0.0020	0.054	-2.89***	11.51
87.09	0.00014	0.016	-0.031***	0.45	-0.0004	0.008	-2.90***	10.27

Table 10: Difference between means and associated effect sizes (using Cohen's D) between the bet-hedge and null model for average early calf survival, average winter calf survival, average calf birth mass and average calf early winter mass. Rows represent each of ten winter severity regimes by average number of severe winter days. The red highlighted row (Regime #7) shows the values simulated for the current weather conditions at Starkey. * P≤0.05, ** P≤0.001, *** P≥0.00001.