



The Importance of Environmental Variability and Transient Population Dynamics for a Northern Ungulate

Sophie L. Gilbert^{1*}, Kris J. Hundertmark², Mark S. Lindberg², David K. Person³ and Mark S. Boyce⁴

¹ Department of Fish and Wildlife Sciences, University of Idaho, Moscow, ID, United States, ² Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, United States, ³ Alaska Department of Fish and Game, Braintree, VT, United States, ⁴ Department of Biological Sciences, Faculty of Science, University of Alberta, Edmonton, AB, Canada

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*Correspondence:

Sophie L. Gilbert
sophiegilbert@uidaho.edu

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The pathways through which environmental variability affects population dynamics remain poorly understood, limiting ecological inference and management actions. Here, we use matrix-based population models to examine the vital rate responses to environmental variability and individual traits, and subsequent transient dynamics of the population in response to the environment. Using Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Southeast Alaska as a study system, we modeled effects of inter-annual process variance of covariates on female survival, pregnancy rate, and fetal rate, and summer and winter fawn survival. To examine the influence of environmental variance on population dynamics, we compared asymptotic and transient perturbation analysis (elasticity analysis, a life-table response experiment, and transience simulation). We found that summer fawn survival was primarily determined by black bear (*Ursus americanus*) predation and was positively influenced by mass at birth and female sex. Winter fawn survival was determined by malnutrition in deep-snow winters and was influenced by an interaction between date of birth and snow depth, with late-born fawns at greater risk in deep-snow winters. Adult female survival was the most influential vital rate based on classic elasticity analysis, however, elasticity analysis based on process variation indicated that winter and summer fawn survival were most variable and thus most influential to variability in population growth. Transient dynamics produced by non-stable stage distributions produced realized annual growth rates different from predicted asymptotic growth rates in all years, emphasizing the importance of winter perturbations to population dynamics of this species.

Keywords: transient population dynamics, ungulate, Sitka black-tailed deer, winter severity, environmental stochasticity, survival, population growth

INTRODUCTION

Identifying key environmental factors that dictate animal population dynamics is a primary goal of ecologists, yet linking changes in environmental conditions to population-level responses remains a central challenge (Gamelon et al., 2014; Maldonado-Chaparro et al., 2018). Environments are complex and many features vary across time and space. Consequently, the effects of environmental variables on dynamics of populations can differ annually, seasonally, and spatially in magnitude and

direction (Coulson et al., 2005). Moreover, those effects may be manifested differently in life history stages within the population, dependent on the species' biology (Gamelon et al., 2014). Because of difficulties in measuring population responses to environmental influences across all life history stages, inference regarding population responses to environmental change is frequently drawn from studies of a single important life history phase, and important covariates of fitness for this life history phase are then assumed to also be the primary factors influencing population dynamics. Yet even strong effects of the environment on life history phase may not matter in the context of population dynamics if those vital rates are relatively unimportant in determining population growth (Gaillard et al., 1998). Likewise, highly influential life-history phases in theory may not vary much in the real world due to evolutionary canalization of life-history patterns (i.e., reduced phenotypic variation due to unknown developmental mechanisms; Gaillard and Yoccoz, 2003).

Animal populations going through an abrupt change in size due to environmental or management actions often have different proportions of animals of each age (i.e., population stage) than populations not going through such perturbations, because the effects of the perturbation on age-specific vital rates often differs. Yet long-standing approaches to prospective and retrospective population analysis (i.e., sensitivity and elasticity analysis and life table response experiments), which are often used to analyze the effects of perturbations on population growth rates, assume the population has reached an asymptotic equilibrium where proportions of population stages are constant (i.e., stable age distribution). Importantly, perturbed populations with a non-stable age distribution often can result in very different annual population growth rates and population abundance than predicted by asymptotic analysis, which is referred to as population momentum (Koons et al., 2006).

Advances in modeling have led to substantial progress in understanding the effects of covariates on vital rates, such as survival (Pollock et al., 1989; Tsai et al., 1999; Blums et al., 2005; Monteith et al., 2013) and reproductive success (Delgiudice et al., 2007; Therrien et al., 2008; Tollefson et al., 2010). In parallel, our understanding of how vital rates affect population dynamics in variable environments has also improved dramatically with the advent of stochastic and density-dependent population models (Grant and Benton, 2000; Hunter et al., 2010; Boyce et al., 2012), life table response experiments (LTREs; Caswell, 2001, 2010), integrated population models (Schaub and Abadi, 2011), and increasingly in recent years, transient population analysis (Koons et al., 2005; Caswell, 2007; Ezard et al., 2010; Maldonado-Chaparro et al., 2018). Yet for many species, such analyses remain elusive due to data limitations, because data on all important life-history phases are required.

In this study, we examined the response of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) vital rates to environmental and individual-level predictor variables, then compare asymptotic and transient analysis of population dynamics to better understand the importance of transience for this population. Sitka black-tailed deer in the coastal temperate rainforest of North America provide an excellent

system for such an examination of transience in response to the environment. Like many ungulates inhabiting temperate and higher latitudes, they are strongly influenced by seasonality and winter stochasticity. As expected for a sub-species of mule deer, Sitka black-tailed deer breed in fall (primary rut occurs in late October through early November, although secondary and tertiary rut cycles can occur for females not bred during the initial cycle), and produce 1 or 2 offspring per litter the following spring, first fawning as 2-year-olds (Johnson, 1987). They are the primary herbivore in the coastal temperate rainforest of Southeast Alaska, and an important source of protein for subsistence hunters, wolves (*Canis lupus*), and black bears (*Ursus americanus*). Winter is thought to limit deer populations in this system (Klein and Olson, 1960; Doerr et al., 2005; Farmer et al., 2006; Person et al., 2009), and industrial-scale timber harvest creates even-aged seral stands with poor winter forage (Alaback, 1982; Farmer and Kirchhoff, 2007), reducing the resilience of deer populations to severe winters, and possibly to predation as well (Farmer et al., 2006; Person et al., 2009). Previous studies have focused almost exclusively on adult female survival (Farmer et al., 2006; Person et al., 2009), without studying reproduction and subsequent fawn survival. This is a troubling gap in knowledge, because juvenile survival drives most observed variation in population growth rates for ungulates (Gaillard et al., 1998, 2000).

Here, we ask the following questions: Which environmental and individual variables are most predictive of survival for adult females and fawns? How do transient versus asymptotic population dynamics differ? And what do environmental effects and the resulting transient population dynamics imply for Sitka black-tailed deer ecology and management, and for ungulate populations in stochastic environments more generally? To answer these questions, we tested a series of hypotheses (**Table 1**) for each adult vital rate (pregnancy, fetal rate, and annual

TABLE 1 | Hypothesized effects of covariates on vital rates for Sitka black-tailed deer, Prince of Wales Island, AK, United States (2010–2013).

Variable	Predicted Vital Rate Response				
	Pregnancy	Fetal rate	Fawn S(t), summer	Fawn S(t), winter	Adult S(t)
Female age	+	+	+	+	+
Female mass (spring)	+	+	+	+	+
Female fat (spring)			+		+
Fawn birth mass			+	+	
Fawn birth date			+	-	
Fawn birth synchrony			+		
Litter size			-		
Sex (female)			+	+	
Winter severity (t)				-	-
Winter severity (t-1)	-	-	-	-	-
Winter(t)*Birthdate				-	
Timber harvest	-	-	-	-	-

Plus (+) signs indicate a hypothesized positive effect on each vital rate, while negative signs (-) indicate a hypothesized negative effect on that vital rate.

survival), and fawn vital rate (summer and winter survival). For fawn vital rates, we hypothesized that fawn survival should be influenced by maternal quality, and thus maternal age, mass, and body fat should increase fawn survival in summer and winter. Likewise, mass at birth should increase summer survival by reducing predation risk (Lomas and Bender, 2007; Johnstone-Yellin et al., 2009; Hurley et al., 2011), and increase winter survival if early mass deficits persist (Loison et al., 1999; Whiting et al., 2010). Similarly, litter size should reduce summer survival through decreased maternal investment, or potentially increased vulnerability to predation (Johnstone-Yellin et al., 2009; Van Vuren et al., 2013). In addition, birth synchrony should increase summer survival through reduced predation risk (but could have a negative effect instead; Sinclair et al., 2000) and enhanced overlap with peak plant nutrition (Langvatn et al., 2004; Parker et al., 2009). We also hypothesized that female fawns would survive at higher rates than males due to less-conspicuous behavior and slower growth rates (Jackson et al., 1972; Loison et al., 1999). In contrast, late-born fawns should be less vulnerable to bear predation as bears focus on salmon in late summer (Hilderbrand et al., 2004), but more vulnerable to winter starvation due to small body size (Loison et al., 1999; Whiting et al., 2010). Finally, we hypothesized that timber harvest would reduce summer fawn survival by concentrating deer and bears in young productive clearcuts; and winter severity and timber harvest could interactively reduce winter fawn survival, as young clearcuts with deep snow provide poor forage, while older clearcuts support little plant biomass (Alaback, 1982; Hanley, 2005; Farmer and Kirchoff, 2007). For adult female deer, we predicted that all vital rates would respond positively to age, body mass, and body fat (Mueller and Sadleir, 1979; Delgiudice et al., 2006, 2007; Johnstone-Yellin et al., 2009), and negatively to timber harvest and winter severity, with potential lagged negative effects of winter in following years (Robinette et al., 1957; Verme, 1977; Fryxell et al., 1991). In terms of overall population dynamics, we expected that adult female survival would have the largest relative influence on population dynamics based on classic elasticity analysis, but that process variation in juvenile survival (i.e., recruitment) should be the highest of all the vital rates, and have the greatest influence on observed population fluctuations between years. Moreover, we predicted that non-stable stage distributions would result in transient dynamics that are quite different than those predicted by asymptotic growth rates.

MATERIALS AND METHODS

Study Area

Our study was conducted from 2010 to 2013, on central Prince of Wales Island, the largest among the many islands of the Alexander Archipelago of Southeast Alaska (Figure 1). The ~420 km² study area is typical of the coastal temperate rainforest of the region, although with gentler topography, milder winter conditions (Figure 2), and more productive forests than many other islands. Nevertheless, topography can be quite rugged due to the limestone and granite bedrock underlying much of

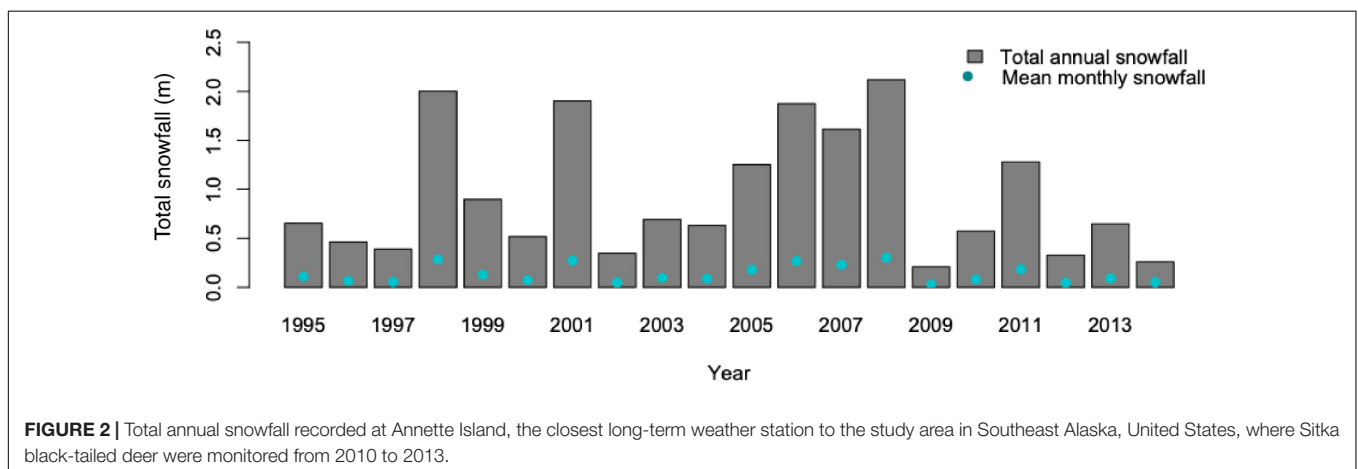
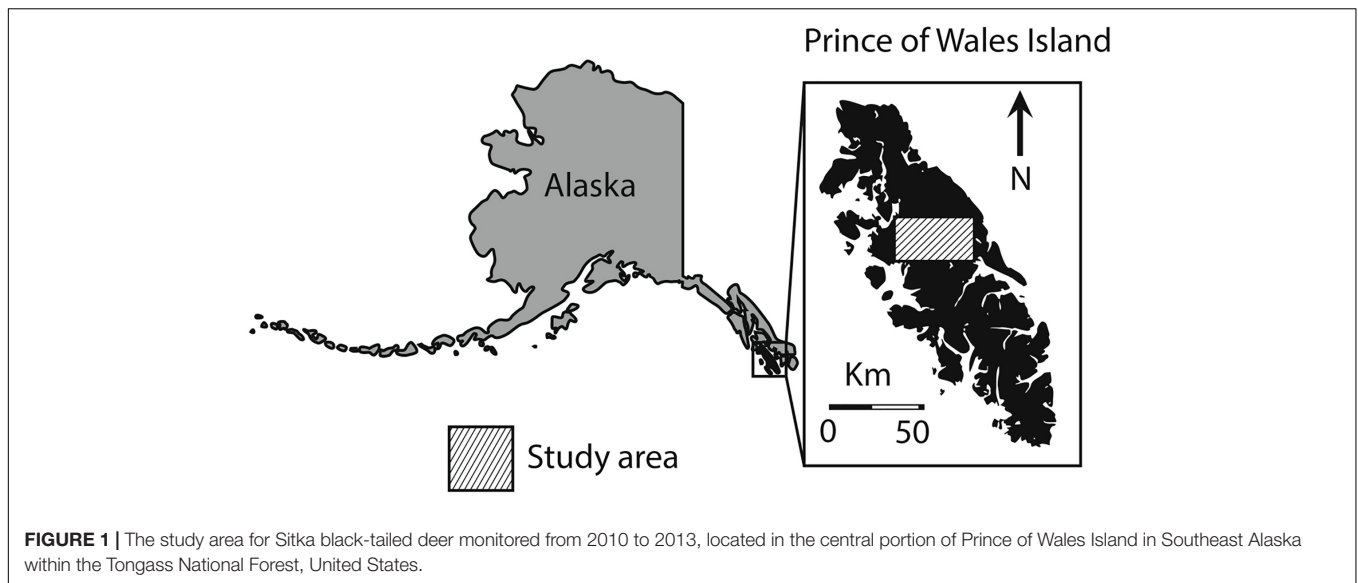
the landscape, ranging from 0 to 1200 m above sea level. Due to moderate annual temperature variation, year-round plentiful precipitation (>3 m per year) falls as rain in summer, and as rain and snow in winter, dependent on temperatures that often fluctuate around freezing. As a result, winter snowfall is highly variable, sometimes persisting at depths < 1 m for weeks at a time even at sea level, but more often quite low at sea-level and increasing with elevation (White et al., 2009; Shanley et al., 2015). Relative to these long-term trends, our study period represented typical summer conditions in all summers (2010, 2011, and 2012), and a mild, moderately severe, and mild series of winters (2010–2011, 2011–2012, and 2012–2013, respectively). Natural habitat types are widely varied, including old-growth forest, numerous lakes, rivers and estuaries, alpine and subalpine vegetation above ~400 m, and muskeg heaths (Alaback and Saunders, 2013).

The favorable environmental conditions relative to the region as a whole have traditionally supported abundant populations of key species, such as Sitka black-tailed deer, black bears, wolves, bald eagles (*Haliaeetus leucocephalus*), and salmon (*Oncorhynchus* spp.) that comprise a predator-prey system that also includes human hunters. In addition, central Prince of Wales continues to be the focus for industrial timber harvest in the Tongass National Forest, including in the study area (U.S. Forest Service, 2008), resulting in disproportionate harvest of productive old-growth forests via large-scale industrial clearcuts, particularly in our study area (Albert and Schoen, 2013). Historical patterns of timber harvest in our study area have produced a fragmented landscape, with some watersheds consisting entirely of old-growth forest, but most watersheds consisting of forest in a variety of seral stages. Timber harvest produces even-aged stands that gradually gain canopy cover and correspondingly lose forage biomass through successional stages, regaining old-growth properties after more than 200 years (Alaback, 1982; Alaback and Saunders, 2013). Of particular importance for deer in our study area is the abundance and large total area of seral stands > 30 years old, now in the stem exclusion stage, resulting in reductions to deer nutritional carrying capacity that are likely to persist for decades across forest management scenarios (Albert and Schoen, 2013; Gilbert et al., 2015). Notably, on northern Prince of Wales Island, where our study area is located, contiguous patches of high-quality old-growth forest have been reduced by over 90%, with average patch size of these contiguous old-growth patches reduced from 264 ha in 1954 to 73 ha in 2004 (Albert and Schoen, 2013), an area comparable to the average female deer's home range (Schoen and Kirchoff, 1985; Yeo and Peek, 1992).

Deer Capture and Monitoring

All animal capture and handling was carried out in accordance with the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14) regulations.

From 2010 to 2012, 61 adult female deer (age 2 years and older) were captured from mid-April through mid-May of each year, and from July 5–25th during 2010 ($n = 20$ in 2010, $n = 20$ in 2011, and $n = 21$ in 2012). We did not capture yearling (age 1 year) animals during this study, but

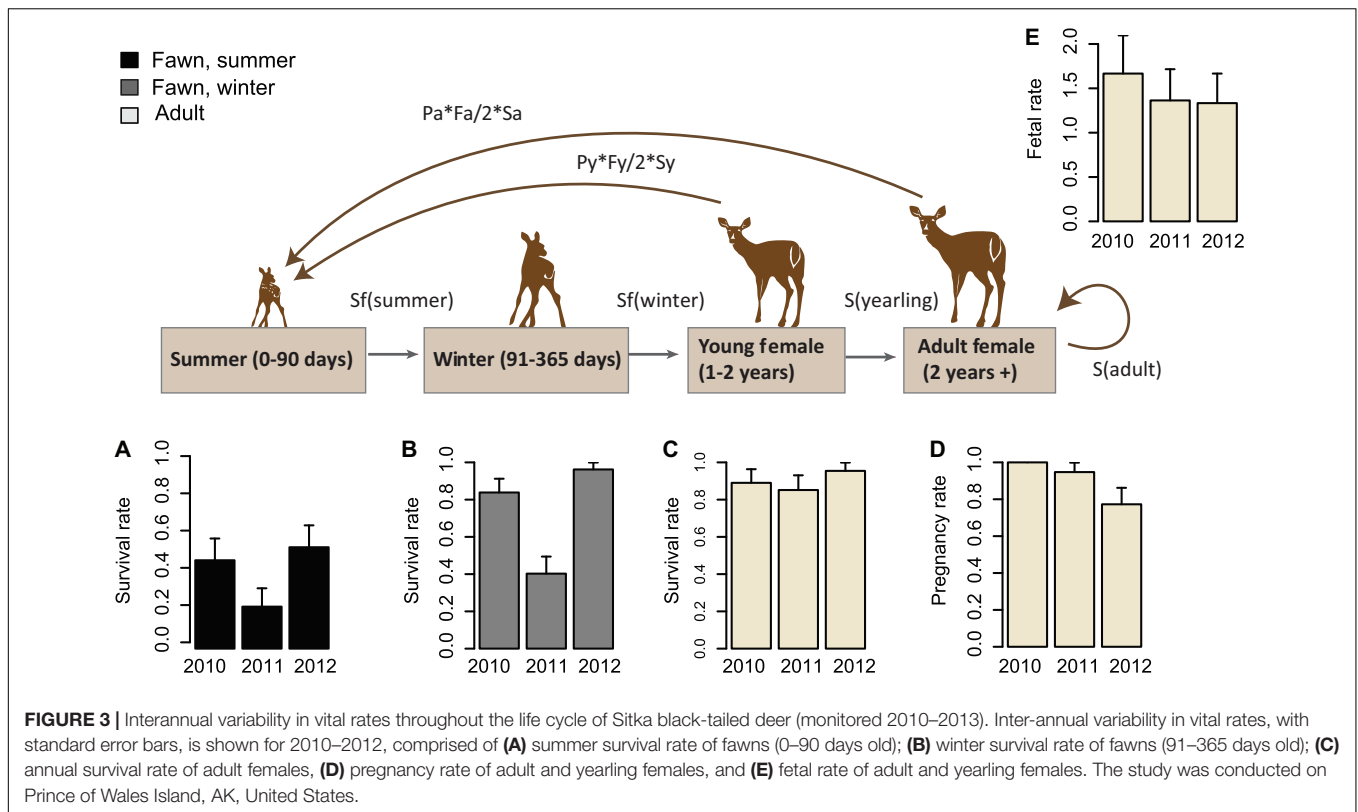


Farmer et al. (2006) and Person et al. (2009) studied deer in adjacent and overlapping study areas and found no difference in survival or causes of mortality between adult and yearling females. At capture, morphological measurements (i.e., heart girth, body length, hind foot length) were measured, blood collected, and body condition and pregnancy assessed using a portable ultrasound machine (Sonosite Titan[®], Sonosite, Bothel, WA, United States). We estimated female body mass based on measured heart girth (Parker, 1987), and ingesta-free body fat based on body mass and measurements from ultrasonography (Cook et al., 2010). Adult females were classified as 2, 3, and 4-plus years old based on tooth wear (Hamlin et al., 2000), but we collapsed 3 and 4-plus year-old animals into a single, adult age class. Adult survival was monitored weekly in summer (April–August 1) and every 2 weeks during the remainder of the year.

If adult females captured pre-parturition ($n = 53$) were pregnant, we attempted to fit them with vaginal implant transmitters (VITs; Advanced Telemetry Systems, Isanti, MN), allowing us to monitor females with VITs daily prior

to parturition, locate the birth site, and capture neonates (Carstensen et al., 2003; Gilbert et al., 2014). Of the adult females successfully fitted with VITs ($n = 49$), we attempted to capture neonates by searching the birth site until 2 fawns were located, or for ≥ 2 h if fewer fawns were located. Neonates were gently restrained with eyes covered to reduce agitation, and were weighed, gendered, measured, and fitted with VHF (all years) and GPS (2012) break-away expandable collars, which fell off after approximately 1–1.5 years. Fawns were subsequently monitored 1–2 times per day from birth until August 1, then every 2 weeks until 1 year of age. The mortality signal was activated after 5 h of collar inactivity, and mortality events were investigated promptly (within 24 h of discovery during monitoring) to determine cause of death.

In total, 45 neonatal deer were captured at birth, while an additional 109 neonates were captured opportunistically along roads and trails and when spotted in meadows and clearcuts. Because mortality is highly age-dependent for neonatal deer, resulting in more vulnerable animals dying at birth or shortly thereafter, we excluded opportunistically captured neonates from



our analysis of summer survival to avoid left truncation of data (Gilbert et al., 2014). In addition, we lacked information on maternal covariates such as maternal age, body mass, and body fat for opportunistically captured fawns. Therefore, because daily survival rates and thus left truncation bias converge in our system at approximately 30 days of age, we included opportunistically captured fawns in our winter fawn survival estimates, increasing our winter sample size to 81 individuals.

Effects of Covariates on Vital Rates

We estimated vital rates, including mean rates across the 3 years of the study and for each year. Vital rates estimated were pregnancy and fetal rates (i.e., number of neonatal fawns per female), summer and winter survival rates for fawns, and annual survival rates for adults. Pregnancy and fetal rate were modeled using generalized linear models in program R (R Core Development Team, 2019) and were treated as binomial and Poisson response variables, respectively (Caswell, 2001; Morris and Doak, 2002).

Only 6 adult female deer died among the 63 monitored over 3 years. This low number of events limited the number of parameters that could be tested simultaneously. Models with fewer than 10 events per variable can produce biased model estimates and Type I predictor selection error (Vittinghoff and McCulloch, 2006). As a result, we only examined the univariate effects of age, mass, bodyfat, and timber harvest regime on adult survival.

Responses of fawn and adult female survival to environmental and individual covariates were modeled using known-fates survival models, implemented in the RMark package in program R (Laake, 2013). We modeled fawn survival in separate summer and winter periods, because vulnerability to predation, sources of mortality, and therefore effects of covariates change from birth through the first year of life. The neonatal period began at birth and continued to 90 days of age, by which age most summer fawn mortality had occurred (Figure 3). During this period, survival was modeled in weekly intervals, with a linear effect of time as survival increases markedly with fawn age (Gilbert et al., 2014). The fall and winter period, henceforth referred to as the over-winter period, extended from 91 to 365 days of age, and survival was considered in 2-week intervals, without an effect of time.

We did not consider adult female body fat as a covariate for pregnancy or fetal rate because body condition was measured in early spring, after pregnancy and fetal rate had already been determined. In addition, we did not have any measures of nutritional condition of fawns prior to winter because they were not re-captured. Therefore, with respect to winter survival of fawns, we included an effect of mass at birth, and back-calculated mass at birth for opportunistically captured fawns by assuming a universal age of 5 days at capture. Many studies age opportunistically captured fawns based on new hoof growth (Sams et al., 1996; Haskell et al., 2007); however, existing hoof growth equations were recently demonstrated to be inaccurate for mule deer (Grovenburg et al., 2014). Instead, we empirically

generated a potential capture age window by re-capturing fawns caught at birth up until the age at which they could no longer be recaptured (11 days), and assigned the median of this period (5 days) as the age at capture (Johnson et al., 2004; Gilbert et al., 2014).

To identify top and competing models for inference, we began with a global covariate model for each vital rate, based on hypothesized ecological relationships described previously. We reduced the global model for each vital rate into subset models with a maximum of 3 covariates per model for fawns and 1 covariate per model for adult females due to our limited sample sizes and numbers of mortality events. Variables that were highly correlated with each other ($r > |0.6|$) were not included in the same sub-models to prevent coefficient bias. For each vital rate, a competitive model set was formed of models with Akaike's Information Criterion adjusted for small sample size (AICc) scores that differed ≤ 2 from the model with the lowest AICc score. We then discarded models with uninformative covariates from the competing model set (Arnold, 2010), defined as models where the model was simply an hierarchical expansion by a single covariate of the top-ranked model with no reduction in log likelihood (Burnham and Anderson, 2002; Arnold, 2010). We did not conduct model validation, as hypothesis-testing rather than prediction was the primary goal of this study, and sample size was limited.

Estimation of Process Variance in Vital Rates and Predictive Variables

Temporal process variation in the vital rates was estimated by fitting a model without covariates for each vital rate, but with a group (strata) effect of year, which we then used to estimate the mean and standard error for each vital rate in each year (i.e., raw variation in vital rates across years; Morris and Doak, 2002; White, 2000). Then, we followed the approach proposed by White (2000) to partition process from sampling variance, implemented in program R. The resulting mean vital rates, with variance partitioned into sampling and process components, were used in subsequent matrices. Temporal process variance in covariates of vital rates was estimated using different approaches for environmental and individual covariates. Variation in individual covariates between years was assumed to contain both process and sampling variance, as estimates depended on the animals sampled. For individual-level predictive variables, we estimated the inter-annual process variance by constructing generalized linear models of each covariate with an effect of year in the model, then used the maximization approach of White (2000) to partition process from sampling variance, as before. To quantify winter severity, we examined variation in total annual snowfall at Annette Island from 1995 to 2014 (Figure 2) as a measure of inter-annual variability and assumed that all observed variance was process variance.

Effects of Vital Rates and Covariates on Population Dynamics

To determine the effects of each covariate on vital rates, we used the fitted relationships from the top model for each vital

rate identified based on AICc score to generate predicted vital rates across a range of each of two times the standard deviation of each predictive variable (calculated as the square root of process variance). If a variable occurred in more than one vital rate model, we perturbed all vital rates affected by that variable simultaneously so that the combined effects of each variable were incorporated into covariate elasticity calculations. For each variable perturbation, we then used the predicted vital rate responses as inputs into a matrix-based population model. The post-breeding model structure included 3 age classes (Figure 3), fawns, yearlings, and adults, with the transition probability for the first age class composed of multiplicative summer and winter survival rates, as discussed above. The matrix structure was specified as follows:

$$\begin{bmatrix} N_{f(t+1)} \\ N_{y(t+1)} \\ N_{a(t+1)} \end{bmatrix} = \begin{bmatrix} 0 & P_y * \frac{F_y}{2} * S_y & P_a * \frac{F_a}{2} * S_a \\ S_{f(s)} * S_{f(w)} & 0 & 0 \\ 0 & S_y & S_a \end{bmatrix} \begin{bmatrix} N_{f(t)} \\ N_{y(t)} \\ N_{a(t)} \end{bmatrix} \quad (1)$$

Where N_j is the number of individuals in age class j at time t , $N_{j(t+1)}$, is the number of individuals in age class j at time $t + 1$, S_j is the survival probability of age class j , and P_j and F_j are the pregnancy rate and fecundity (as females per female) respectively, of an individual of age class j . Because we did not capture any yearling individuals, we assumed that survival of yearlings was equal to that of adult females, as found in a previous study adjacent to our study area (Farmer et al., 2006). Pregnancy and fecundity of yearlings was measured during the course of this study, despite the fact that no yearlings were captured, because animals that were captured in the spring and aged as 2 years old were primiparous yearlings about to turn 2 (Figure 3).

For comparison with the perturbed matrix for each variable, we constructed a baseline matrix, with mean vital rates calculated from the top-ranked models and covariates held at mean values. We then calculated the covariate elasticity of each vital rate as the percent difference in the dominant eigenvalues (i.e., growth rates, λ) of the two matrices:

$$Ec = \frac{\lambda_{\text{pert}} - \lambda_{\text{base}}}{\lambda_{\text{base}}} \quad (2)$$

Where Ec is the covariate elasticity, λ_{base} is the dominant eigenvalue of the baseline matrix, and λ_{pert} is the dominant eigenvalue of the perturbed matrix [which is wonderfully dynamic like transient abundances]. We examined the effects of a positive versus negative perturbation to each covariate, resulting in positive and negative changes to λ_{pert} depending on the sign of the covariate coefficient. We calculated elasticities of the vital rates, and contributions of vital rates to observed inter-annual variability in growth rate (LTRE; Caswell, 2001; Morris and Doak, 2002), using the popbio package (Stubben et al., 2012) in program R. Elasticities of vital rates were calculated from the baseline matrix, λ_{base} . Contributions of vital rates to variation in growth rate (i.e., LTRE; Caswell, 2001) were based on sensitivity analysis of vital rates within the mean matrix between a treatment matrix and the baseline matrix. In this case, the vital rates for the treatment matrix where simply baseline vital rates reduced by 2 standard deviations, with SDs calculated from estimated process

TABLE 2 | Estimates of vital rates for across the period of the study (2010–2013) for Sitka black-tailed deer, Prince of Wales Island, AK, United States.

Vital Rate	Estimate	Total σ^2	Process σ^2	N
Pregnancy Rate	0.89	0.03	0.004	53
Fetal rate (fawns per female)	1.45	0.07	<0.001	32
Fawn survival, 1–90 days	0.41	0.06	0.01	45
Fawn survival, 91–365 days	0.73	0.17	0.08	82
Adult survival, 1–365 days	0.90	0.005	<0.001	61

Estimates are shown as means with total variance, process variance, and sample size (N).

variance for each vital rate (Table 2). If a vital rate had zero estimated process variance, it was not perturbed.

Sex was a covariate of fawn survival, yet we used a single-sex, all-female model for prediction of the effects of covariates, including sex. Perturbing the frequency of male versus female fawns would affect fawn survival and would therefore change the fecundity terms in our population model (i.e., number of female fawns per female at birth) in our population model. Because as we found no process variance (<0.001) in sex ratio between the years of our study, we not vary the sex ratio of fawns in our models.

Transient Analysis

Because our population was thought to be strongly affected by winter severity, which differentially affects stage class, and because we do not know how density dependence affects vital rates included in our population matrices, it is highly unlikely that the population ever achieves the stable stage distributions dictated by asymptotic analysis of our three annual Leslie matrices. To better understand how important such non-stable-stage effects on population growth might be, we conducted transient analysis. First we, constructed a simulation, in which we stochastically generated 10,000 initial stage distributions for the first year of our study (2008–09, a mild winter year following 3 successive severe winters), then projected this population structure through the subsequent annual matrices, which represented a year with a mild winter in year t (2010–2011), followed by a year with a severe winter (2011–2012), followed by a year with a mild winter (2012–2013). For each population run, we calculated population size for each stage in each year, transient population growth [simply $N(t+1)/N(t)$], reactivity (a measure of population density in the first year following perturbation, calculated as transient growth divided by asymptotic growth of the annual matrix), and inertia, a similar metric indicating the ratio of maximum population size achieved due to both transient and population dynamics compared to that achieved via asymptotic growth alone (Koons et al., 2007; Stott et al., 2012). Following initial analysis, inertia was revealed to be equivalent to reactivity for this population, since maximum transient population size relative to asymptotic dynamics was achieved in year $t = 1$, and inertia was therefore not included in our final analysis. These resulting distributions of population size, transient growth, and reactivity were used to generate the median and 95% confidence intervals for these metrics. In addition, we examined the minimum and maximum potential

influences of transient dynamics for each annual matrix using the minimum attenuation and maximum amplification metrics described in Stott et al. (2012), which also allows for calculation of which population stage contributed most to attenuation and amplification relative to asymptotic dynamics.

RESULTS

Vital Variability and Response to Predictive Variables

Pregnancy and Fetal Rate

The average pregnancy rate for adult female deer was 0.89 (Total variance = 0.03, process variance = 0.009). Vital rates varied across years (Table 2 and Figure 3). Females had pregnancy rates of 1.0 in 2010, 0.95 in 2011, and 0.77 in 2012.

The average fertility rate for pregnant females was 1.45 fawns per female (total variance = 0.07, process variance < 0.001), implying a rate of 0.72 female fawns per female if a 1:1 gender ratio is assumed. The rate of female fawns per female measured from our captured fawns was 0.625 female fawns per female ($SE = 0.10$), with an upper 95% confidence interval of 0.82, leading us to accept the 1:1 gender ratio assumption. Among years, the fertility rate was 1.67 fawns per female ($SE = 0.43$) in 2010, 1.36 ($SE = 0.35$) in 2011, and 1.33 ($SE = 0.33$) in 2012.

Variables that affected probability of pregnancy were the severity of the proceeding winter as measured by total snowfall [winter($t-1$)], adult female age, and timber harvest of the watershed, with the best-supported model including winter ($t-1$) and timber harvest (Table 3). Adult female age had a positive effect on probability of pregnancy, as did occupancy of a timber-harvested watershed, while a winter with greater total snowfall reduced the probability of pregnancy in the following spring. Fetal rate was not strongly affected by any covariates; the null model was top-ranked, although a positive effect of female age ($\Delta AICc = 1.24$; Table 3) and female mass ($\Delta AICc = 1.83$) also received support. Female age and female mass were positively correlated for pregnant females ($r = 0.60$, $p < 0.01$) and for females where fawns were captured ($r = 0.57$, $p < 0.01$), and as a result, female age and female mass were not simultaneously included as covariates in any vital rate models. Based on the univariate analysis of covariates of female survival, there was support for negative effects of female mass and age on survival (i.e., younger, lighter-weight females survived with higher probability; Table 3).

Adult Survival Rate

As previously discussed, annual adult survival was high and showed little process variance, averaging 0.90 (total variance = 0.005, process variance < 0.001) for the study period, and varying little between years, and was estimated as 0.89 ($SE = 0.07$) in 2010, 0.85 ($SE = 0.08$) in 2011, and 0.95 ($SE = 0.04$) in 2012. The largest source of mortality ($n = 3$) was from hunting, with an average mortality rate of 0.05 ($SE = 0.03$), followed by a 0.03 ($SE = 0.02$) mortality rate from malnutrition ($n = 2$), and a 0.02 mortality rate from black bear predation ($n = 1$, $SE = 0.02$). Wolf mortality was not recorded for any

TABLE 3 | Ranked vital rate models within 2 AICc units of the top models of vital rates for Sitka black-tailed deer during the period of the study (2010–2013), Prince of Wales Island, AK, United States.

Model Equation	β_1	β_2	β_3	$\Delta AICc$
Probability of pregnancy				
$P \sim \beta_1(\text{Logged}) + \beta_2(\text{Winter}_{t-1})$	2.49 (1.19)	-3.07 (1.55)	–	0
$P \sim \beta_1(\text{Logged}) + \beta_2(\text{Winter}_{t-1}) + \beta_3(\text{Age})$	2.27 (1.22)	-2.99 (1.57)	1.24 (0.90)	0.12
Number of fetuses per female				
$F \sim 1$	–	–	–	0
$F \sim \beta_1(\text{Age})$	0.20 (0.19)	–	–	1.24
$F \sim \beta_1(\text{Mass})$	0.01 (0.02)	–	–	1.83
Fawn survival summer, 1–90 days				
$S(t)_S \sim \beta_1(\text{Mass}) + \beta_2(\text{Sex})$	2.48 (0.97)	0.90 (0.56)	–	0
$S(t)_S \sim \beta_1(\text{Mass})$	2.12 (0.92)	–	–	0.51
$S(t)_S \sim \beta_1(\text{Mass}) + \beta_2(\text{Winter}_{t-1})$	2.34 (0.95)	0.74 (0.62)	–	1.18
$S(t)_S \sim \beta_1(\text{Mass}) + \beta_2(\text{B.date})$	2.08 (0.92)	0.03 (0.03)	–	1.65
$S(t)_S \sim \beta_1(\text{Mass}) + \beta_2(\text{Sync})$	2.12 (0.91)	0.33 (0.40)	–	1.91
Fawn survival winter, 91–365 days				
$S(t)_w \sim \beta_1(\text{Winter}_t) + \beta_2(\text{B.date})$	-3.27 (0.69)	-0.06 (0.02)	–	0
$S(t)_w \sim \beta_1(\text{Winter}_t) + \beta_2(\text{B.date}) + \beta_3(\text{B.date} * \text{Winter}_t)$	-1.60 (1.34)	0.02 (0.06)	-0.08 (0.06)	0.14
Adult survival 1–365 days				
$S(t) \sim \beta_1(\text{Mass})$	-0.19 (0.07)	–	–	0
$S(t) \sim \beta_1(\text{Age})$	-1.67 (0.74)	–	–	1.77

Competitive models are shown with parameter estimates and (standard errors), and difference in AICc score from top-ranked model.

adult deer monitored during this study, despite wolf predation acting as a major source of mortality for deer monitored in the same study area 10 years previously (Person et al., 2009; Alaska Department of Fish and Game, unpublished data). Wolves were at low numbers and restricted distributions during the course of this study due to high harvest pressure (Gilbert et al., 2015; Alaska Department of Fish and Game, 2017).

Fawn Survival Rate

Fawn survival was lowest during the summer, due primarily to predation by black bears, and highly variable between years. Average survival in summer was 0.41 across years (total variance = 0.06, process variance = 0.01), and annual summer survival rates were 0.47 in 2010 ($SE = 0.13$), 0.23 in 2011 ($SE = 0.11$), and 0.54 in 2012 ($SE = 0.13$). Across all years, mortality rates were 0.46 ($n = 21$, $SE = 0.08$) due to black bear predation, and 0.11 ($n = 6$, $SE = 0.05$) due to other causes. Other causes of mortality included unknown predation ($n = 1$), eagle predation ($n = 1$), drowning ($n = 1$), and premature birth ($n = 3$). As before, because maternal mass and age were correlated among the fawns sampled ($r = 0.56$), they were not included in the same models. In addition, synchrony of births was lower in timber harvested watersheds ($p = 0.015$), although the two variables were only moderately correlated ($r = 0.36$).

Summer fawn survival, from birth through 90 days of age, was affected by gender and birth mass. In the top-ranked survival model, female fawns had a higher survival probability male fawns, as did fawns that weighed more at birth (Table 3 and Figure 4A). Other competitive models included a positive effect of birth asynchrony on survival, indicating that fawns born more synchronously survived at lower rates, and a positive effect of winter severity in the previous year, indicating that fawns

produced following a severe winter survived better. While there were no strongly correlated covariates, there was a statistical relationship between timber harvest of watershed and birth synchrony, with more asynchronous births in timber harvested watersheds ($r = 0.34$, $p = 0.015$).

During the winter months, fawn survival was determined primarily by malnutrition-caused mortality, which occurred only during the winter of 2011. Across the three years of the study, the average winter survival rate was 0.73 (total variance = 0.17, process variance = 0.08), due to a mortality rate of 0.21 ($n = 16$, $SE = 0.05$) from malnutrition, 0.03 ($n = 2$, $SE = 0.02$) from wolf predation, 0.02 ($n = 1$, $SE = 0.02$) from bear predation (in late September), and 0.03 ($n = 2$, $SE = 0.02$) due to other causes ($n = 1$ car collision, $n = 1$ illegal hunting). Among years, winter survival rates were high in 2010 ($M = 0.84$, $SE = 0.07$) and 2012 ($M = 0.96$, $SE = 0.04$), and quite low in 2011 ($M = 0.40$, $SE = 0.09$).

Winter fawn survival, from 91 through 365 days of age, was strongly affected by winter severity and birthdate. The top-ranked model supported negative effects of winter severity and birthdate, indicating that late-born fawns were at greater risk of mortality, as were fawns during high-snowfall winters. In addition, a competing model supported an interactive, negative effect of winter severity and birthdate, indicating lower survival during severe winters and for late-born fawns (Table 3 and Figure 4B).

Effects of Vital Rates on Asymptotic Population Dynamics

Analysis of the baseline population model indicated that the average population growth rate for the study period was

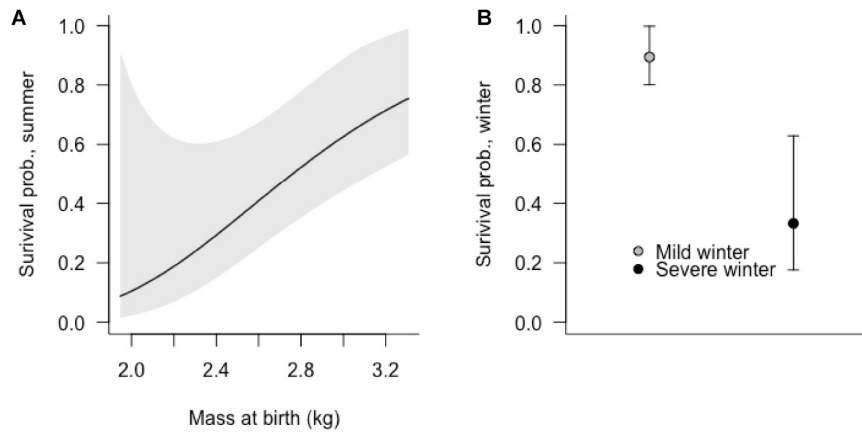


FIGURE 4 | The effects of (A) birth mass of Sitka black-tailed deer fawns on summer survival (0–90 days old), and of (B) occurrence of a severe winter on fawn winter survival (91–365 days old), shown with 95% confidence intervals. The study was conducted 2010–2013, on Prince of Wales Island, AK, United States.

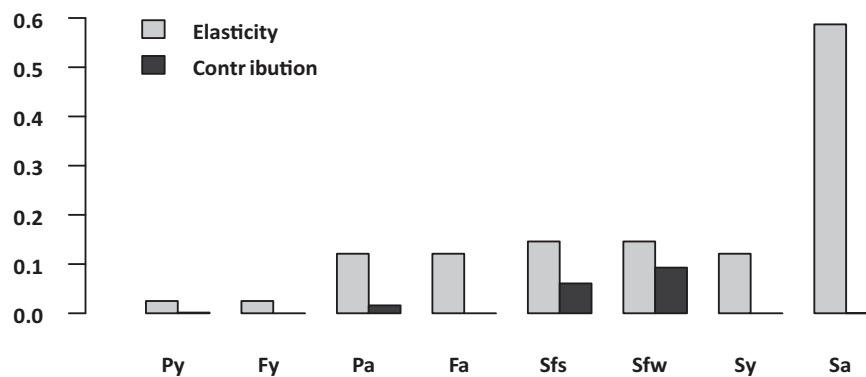


FIGURE 5 | Sitka black-tailed deer vital rate elasticity versus contributions to observed annual variability in asymptotic growth rate, where P_y and F_a denotes pregnancy of yearlings and adults, F_y and F_a denoted fertility (females per fawn) of yearling and adults, and $S_f(s)$, $S_f(w)$, S_y , and S_a denote survival of age classes fawn (days 1–90), fawn (days 91–365), yearling, and adults. The study was conducted 2010–2013, on Prince of Wales Island, AK, United States.

distinctly positive, with $\lambda = 1.08$, despite the harsh winter of 2011. Annual estimates of deterministic population growth rates were 1.17 in 2010, 0.92 in 2011, and 1.18 in 2012. The most influential vital rate based on deterministic elasticity values (Figure 5 and Supplementary Table 1) was adult female survival, followed by summer and winter fawn survival, survival of yearlings, fertility of adults and yearling, and pregnancy of adults and yearlings. In contrast, when vital rates were perturbed based on process variation, relatively high levels of process variation resulted in winter fawn survival contributing most to variation in inter-annual growth rate, followed closely by summer fawn survival, then by adult and yearling pregnancy rate, with other vital rates contributing much less due to almost no process variation (Figure 5 and Supplementary Table 1).

Transient Population Dynamics

Transient simulation analysis indicated that initial stage structure can cause differences in realized growth compared to growth predicted from asymptotic analysis (Figure 5). Realized median

growth rate was 1.29 (95% CI = 1.13, 1.43) in 2010, 0.92 (95% CI = 0.89, 0.95) in 2011, and 1.12 (95% CI = 1.11, 1.12) in 2012, indicating that the initial uncertainty we included in stage structure attenuated with time. These transient growth rates were different from those predicted by asymptotic dynamics, resulting in reactivity ratios relative to asymptotic dynamics of 1.10 (95% CI = 0.96, 1.22) in 2010, 0.99 (95% CI = 0.97, 1.04) in 2011, and 0.93 (95% CI = 0.93, 0.94) in 2012. This simulation did not include uncertainty in yearly vital rate values, so potential variability of growth rates could be considerably higher. Analysis of population inertia indicated that both maximum attenuation and amplification relative to asymptotic growth rate occurred in the first time-step following perturbation of all annual matrices. For the 2010, 2011, and 2012 annual matrices, maximum attenuation was 1.49, 1.73, and 1.36 respectively, resulting in a realized growth rate of 1.75, 1.58, and 1.62, and with the adult female stage, fawn stage, and fawn stage contributing most to amplification differences. Yearly matrix maximum attenuations for 2010, 2011, and 2012 were 0.34, 0.08, and 0.41 respectively, resulting in realized growth rates of 0.40, 0.07, and 0.49, and

TABLE 4 | Maximum possible amplifications and attenuations of Sitka black-tailed deer population projection matrices observed during this study (2010–2013), along with number achieved at max/min [N(t)], and stage making the greatest contribution.

Matrix	A Mild($t-1$)Mild (t)	A Mild($t-1$)Severe (t)	A Severe($t-1$)Mild (t)
Max amplification	1.49	1.73	1.36
N(t)	1.75	1.58	1.63
Stage	Adult female	Fawn	Adult female
Max attenuation	0.34	0.08	0.41
N(t)	0.40	0.07	0.49
Stage	Fawn	Fawn	Fawn

All min/max values were achieved within one timestep. The study was conducted on Prince of Wales Island, AK, United States.

with the highest level of contributions coming from fawns for all matrices (Table 4).

DISCUSSION

Winter severity emerged as a dominant influence on population dynamics for Sitka black-tailed deer, based on vital rate models and analysis of population dynamics, and resulting from high vulnerability of fawns to mortality in severe winter conditions. While many of our hypotheses regarding the primary influences on deer vital rates and population dynamics followed expectations for a northern ungulate, there were also some intriguing and unexpected outcomes from our analyses. For adult females, probability of pregnancy and fetal rate were higher for older females, as predicted, while adult female mass positively affected fetal rate. These results agree with life-history theory, in which older and larger females of long-lived species typically produce more offspring at more frequent intervals (Hamel et al., 2009; Lindberg et al., 2013). While reproductive senescence is thought to occur in Sitka black-tailed deer (Johnson, 1987), our study was not longitudinal across the lifetime of a deer, so the importance of senescence was not possible to determine. Interestingly, there was a mild positive effect of the binary timber harvest variable on probability of pregnancy; in addition, synchrony of births was negatively affected by timber harvest, indicating that some feature of these altered watersheds affected deer conception probability and timing and suggesting the need for further inquiry. Based on our univariate analysis of covariates of adult survival, female mass negatively affected survival of adult females, likely because hunters selected for larger individuals. Hunting was the primary cause of death for adult females in our study, and larger animals are typically preferred by hunters (Milner et al., 2007; Brinkman et al., 2009). Thus, large body mass could decrease adult female risk from natural causes (as has been documented in many other systems) but increase risk from human hunting.

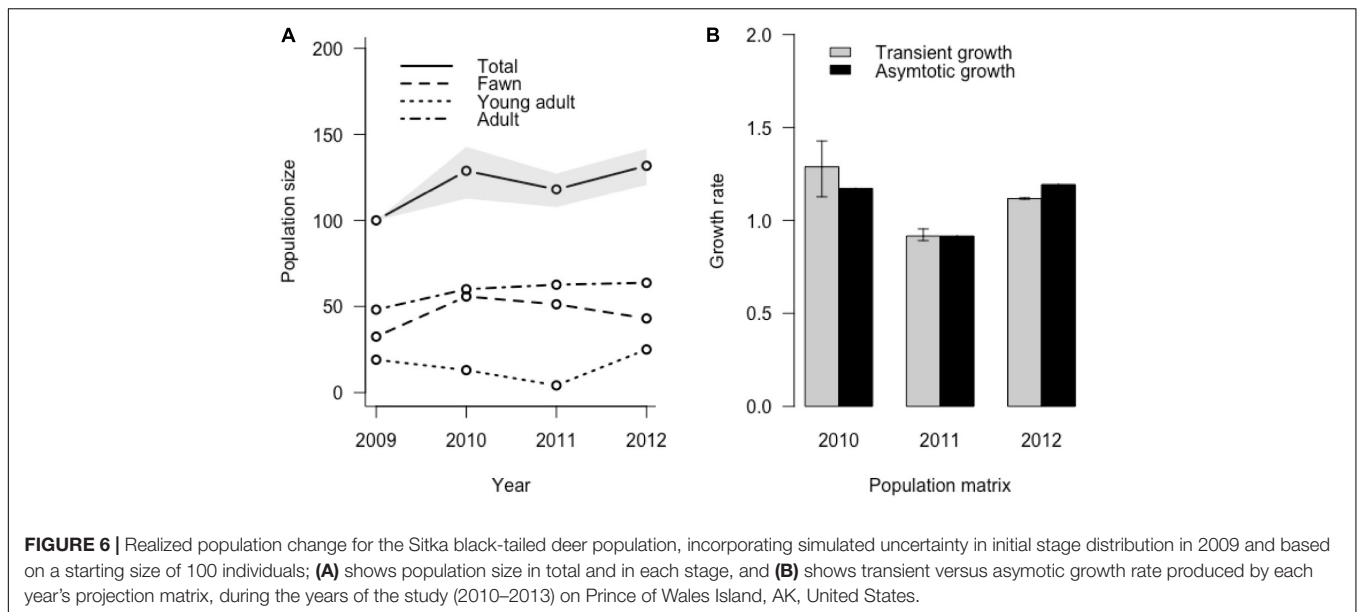
Summer fawn survival was the lowest survival rate, with more than half of all fawns dying before 3 months of age on average (Table 2), primarily from black bear predation. Summer fawn mortality risk was negatively affected by birth mass and fawn gender, with larger fawns and female fawns surviving with higher probability. Behavioral differences between male and female

fawns have been observed, with male fawns engaging in more conspicuous behaviors (i.e., active more of the time; Jackson et al., 1972), likely increasing detection probability by bears. In addition, synchrony of birth decreased summer survival, possibly because bears actively search for fawns only during the peak of births. Surprisingly, the severity of the previous winter positively affected summer fawn survival, possibly because low-quality adult females were selectively removed from the population, along with their unborn offspring, or lost fetuses prematurely and did not give birth at all (as evidenced by the low pregnancy rate in 2012). Bear predation risk appears to be linked to nutrition of fawns, given the strong effect of fawn mass at birth on summer survival, and thus is likely partially compensatory. Yet other expected nutritional effects were not supported; maternal spring body fat did not predict subsequent fawn survival, suggesting that perhaps females conserve body fat at the expense of fawn mass at birth (i.e., the “selfish cow” hypothesis, Clutton-Brock et al., 1989; Therrien et al., 2008; Parker et al., 2009).

In contrast, overwinter fawn mortality varied greatly from year to year, and was almost entirely driven by malnutrition in the single harsh winter, with very high fawn survival during the other years, beyond our expectations. Late-born fawns, which enter winter at smaller sizes and with fewer body reserves, were at greater risk of malnutrition during the harsh winter but not during other winters. Intriguingly, we recorded no effect of birth mass, demonstrating that fawns were likely able to recover from early deficits in body mass. While there was no support for an effect of timber harvest regime of watershed on winter survival, the connection between timber harvest and birth asynchrony indicates that timber harvest can affect birth timing, and merits further investigation given the importance of birthdate for surviving harsh winters.

While timber harvest did have a negative effect on fawn and adult female survival based on coefficient values in models in which it occurred, the standard errors of the term were high, leading to the exclusion of the term from final models. Timber harvest regime of watersheds is a very coarse variable, homogenizing variation in seral stage and corresponding nutrition within deer home ranges. In addition, deer select habitat from within the home range (Johnson, 1980), and may be able to increase access to nutrition through selection (Parker, 2003). Age and configuration of harvested stands, and quality and size of remaining old-growth forest patches, interactively drive deer selection in this study area in winter (Gilbert et al., 2017), and are likely important in determining winter survival. For example, Brinkman et al. (2011) found that deer density declined by 30% after 3 successive severe winters, using a study area overlapping ours and with largest declines in timber-harvested watersheds. A detailed analysis of winter habitat selection that included stand-level variation in seral stage, biomass, and snow depth was conducted in 2017 (Gilbert et al., 2017), and efforts to better characterize timber-harvested habitat and its effects on deer are ongoing (Shanley et al., in review; Gilbert et al., 2015), but linking habitat selection or use to fitness outcomes and population dynamics is an important next step.

Major limitations of this study are its relatively short duration compared to the lifetime of a deer, the correspondingly small



number of winters observed, the lack of knowledge regarding population structure or density, and the lack of detailed information available regarding timber harvest for the different age classes sampled. The negative effects of winter we document here are the result of only 3 years of study, which were by no means as extreme as previously documented severe winters (Brinkman et al., 2011). In such very severe winters, adult female survival can be greatly reduced (Alaska Department of Fish and Game, 2013), whereas we documented only 2 deaths from malnutrition during the severe winter in our study, with no statistical effect on adult female survival. For example, Brinkman et al. (2011) documented a 30% decline in deer density over 3 years, equivalent to a mean annual growth rate of 0.89, lower than our lowest calculated annual growth rate of 0.92. In addition, winter severity could interact with deer density relative to carrying capacity to influence survival and growth rate response (Bowyer et al., 2014), which we were not able to measure during the course of this study. Therefore, it is likely that the effects of severe winters on population growth can be much greater than documented here, due to reduced adult female survival, a highly influential vital rate in the population, and also dependent on stage structure entering the winter, as indicated by a minimum possible transient growth rate from our harsh winter matrix of 0.07 (i.e., drastic population decline). Likewise, a larger wolf population, typical during years prior to our study, likely would reduce winter survival of fawns and adults, particularly during severe winters, but we were unable to document such winter-predation interactions due to a greatly reduced wolf population size during our study (Person et al., 2009; Gilbert et al., 2015; Alaska Department of Fish and Game, 2017). Wolf abundance also may affect the influence of habitat covariates on vital rates if deer alter behavior and select lower-nutrition habitats to avoid risk of predation at higher wolf densities (Chamaillé-Jammes et al., 2014). In addition, while timber harvest is the dominant disturbance mechanism in the temperate rainforest ecosystem of our study

area, which has been disproportionately harvested compared to other parts of the region (Albert and Schoen, 2013), our sampling methods did not allow us to conduct detailed analysis of habitat use for all deer included in the study (e.g., fawns sampled opportunistically did not have GPS-collared mothers to provide spatial locations). As a result, we were only able to include timber harvest as a binary, watershed-level predictive variable in our models, which undoubtedly greatly reduces our ability to make inference about how this important source of disturbance affects deer.

Both asymptotic and transient analysis of growth yielded broadly similar pictures of depressed growth during harsh winters (Figure 6), but with differences in stage structure contributing to considerable divergence in transient versus predicted asymptotic growth. While adult female survival is highly influential in determining inter-annual differences in asymptotic population growth in theory, it is neither highly variable nor highly responsive to environmental influences in our system, nor does it contribute substantially to variability in population growth rate. This conforms to other studies of ungulate population dynamics (Gaillard et al., 1998, 2000). In contrast, juvenile survival is strongly influenced by environmental and individual covariates, primarily by mass at birth and thus presumably nutrition during summer and early fall, and winter severity during the winter. Thus, variation in environmental covariates can influence population growth rate most strongly through changes in fawn survival rather than adult survival. It is important to note, however, that when an extreme event (i.e., very deep, persistent snow in winter) does reduce adult survival, the same event is likely to reduce juvenile survival and pregnancy rates much more, resulting in a compounded negative impact to the transient population growth rate via a change in stage structure and a change in vital rates (Coulson et al., 2005; Figure 5).

We were unable to fully investigate the demographic impact of extreme weather events in this study, because such an

extreme event did not occur during the three years of this work. Given projections for increased stochasticity and severity of weather under future climate change scenarios, such compounding, multi-vital-rate effects of stochastic weather should prove highly influential for ungulate populations. In this ecosystem, average winter snowfall is projected to decrease, while severity of stochastically occurring major storms may increase (Shanley et al., 2015), potentially leading to greater swings in deer population size as series of mild winters lead to high population densities, which then experience density-dependent negative impacts of occasional severe winters. Although survival of adult female ungulates is evolutionarily canalized against environmental variation (Gaillard and Yoccoz, 2003), extreme events can overwhelm the resilience of this key vital rate (Brinkman et al., 2011), causing large demographic impacts through joint reductions of adult and juvenile survival. Understanding and predicting the effects of increased frequency of extreme events, and the interactive role that other environmental influences such as an anthropogenic habitat change could play in determining population response, is therefore an emerging challenge for population ecology and management.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by Institutional Animal Care and Use Committee University of Alaska Fairbanks.

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AUTHOR CONTRIBUTIONS

All authors carried out the study design. SG and DP carried out the data collection. SG carried out the data analysis with planning and feedback from all other authors. SG wrote the manuscript with editing by all other authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.531027/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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