

Using multistate capture–mark–recapture models to quantify effects of predation on age-specific survival and population growth in black-tailed deer

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Abstract Effective species management and conservation relies on accurate estimates of vital rates and an understanding of their link to environmental variables. We used multistate capture–mark–recapture models to directly quantify effects of predation on age-specific survival of black-tailed deer *Odocoileus hemionus columbianus* in California, USA. Survival probabilities were derived from individual encounter histories of 136 fawns and 57 adults monitored over 4 years. Based on results from our survival analysis we parameterized a Lefkovich matrix and used elasticity analyses to investigate contributions of mortality due to predation to changes in population growth. We found strong evidence for age-specific survival including senescence. Survival of females >1 year old was consistently low (0.56 ± 0.18 for yearlings, 0.77 ± 0.13 for prime-aged females, and 0.55 ± 0.08 for senescent

individuals), primarily due to high puma *Puma concolor* predation during summer. Predation from black bears *Ursus americanus* and coyotes *Canis latrans* was the primary cause for low annual survival of fawns (0.24 ± 0.16). Resulting estimates of population growth rates were indicative of a strongly declining population ($\lambda = 0.82 \pm 0.13$). Despite high sensitivity to changes in adult survival, results from a lower-level elasticity analysis suggested that predation on fawns was the most significant individual mortality component affecting population decline. Our results provide a rare, direct link between predation, age-specific survival and the predicted population decline of a common ungulate species. The magnitude of predation was unexpected and suggests that ungulates in multi-predator systems struggle to cope with simultaneous reductions in survival probabilities from predators targeting different age classes.

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Introduction

Dynamics of stable ungulate populations are characterized by high and constant adult female survival together with variable juvenile survival and recruitment (Gaillard et al. 2000). Any variation in either bottom-up or top-down effects can upset this pattern and result in significant population fluctuations. Understanding how bottom-up and top-down effects influence vital rates and thus shape the dynamics of animal populations is therefore one of the central questions in ecology (Sinclair and Krebs 2002). The relative importance of bottom-up versus top-down effects is of specific interest for ungulates that are part of complex

communities involving multiple species, both prey and predators, as well as seasonal variation in their environment and associated food availability. How predation influences population dynamics of ungulates in such systems remains controversial, although recent syntheses highlight that its impact will vary with site-specific characteristics as well as time and space (Hopcraft et al. 2010).

Quantifying the direct effect of predation is difficult. For example, how predators affect prey populations depends on environmental variables such as landscape heterogeneity, climate, and anthropogenic disturbances (Hebblewhite et al. 2005; Wilmers et al. 2007), prey body size and population age structure (Sinclair et al. 2003; De Roos et al. 2008), predator and prey composition and relative abundances and type of functional and numerical responses (Creel and Christianson 2008; De Roos et al. 2008), as well as species-specific behavioural traits including antipredator or hunting strategies (Sih et al. 1998). Few studies have thus been able to properly quantify the direct impact of predation on the dynamics of age-structured ungulate populations (e.g., Festa-Bianchet et al. 2006; Gervasi et al. 2012).

Capture–mark–recapture (CMR) models using known-fate encounter histories of marked individuals provide a powerful approach to directly link environmental variables including predation to changes in survival probabilities. By accounting for the detection probability of individuals as well as their transitions from one state to another (e.g., from alive to dead), multistate CMR models address many of the statistical limitations of other survival analyses (Lebreton et al. 2009). Of particular interest for studies aiming to quantify the direct effects of cause-specific mortality on survival probabilities are more recent CMR models in which each cause of mortality can be directly estimated (Schaub and Pradel 2004).

Quantifying the effect of predation is especially relevant for medium sized ungulates where a shift between top-down regulation prevalent in small-bodied species and bottom-up regulation more typically associated with large-bodied species may occur (Sinclair et al. 2003; Hopcraft et al. 2010). Mule *Odocoileus hemionus* and black-tailed deer *O. h. columbianus* in North America are of specific interest in this respect. They are of intermediate size, typically co-occur with a range of other ungulate and predator species and their populations across western North America have exhibited long-term population fluctuations that remain poorly understood, particularly with respect to predation (Ballard et al. 2001; Forrester and Wittmer 2013). Deer are also known to have highly age-structured populations and variation of predation among these age classes may strongly influence their vital rates and population growth (Gaillard et al. 1998; Forrester and Wittmer 2013).

We used data from a 4-year study of marked black-tailed deer (136 fawns, 57 adult females) in California, USA, to quantify the direct effects of predation on age-specific survival probabilities as well as associated dynamical consequences. We focused on age-specific survival and predation because black-tailed deer co-occurred with a diverse community of predators of varying body sizes that had potential to prey on different age classes (Sinclair et al. 2003). We first estimated the spatial and temporal variation in cause-specific mortality rate in each age class using a multistate CMR model (Schaub and Pradel 2004) adjusted for encounter histories obtained from telemetry studies. We then used resulting estimates of survival and other vital rates to estimate the asymptotic population growth rate (λ) from a Lefkovich matrix (Caswell 2001). Finally we used both first-order and lower-level elasticity analyses to determine the degree to which age-specific mortality due to predation affected population growth.

Methods

Study area

Our study area was located in the Coastal Mountains of north-western California. The area encompassed approx. 1,000 km², the majority of which fell within the Mendocino National Forest (39°45'N, 122°58'W, Fig. 1). Two easily accessible ridges (referred to as FH7 and M1) divided the study area into 3 distinct watersheds. Elevations ranged from approximately 400 to 1,900 m a.s.l. on ridgetops. Climate in the study area can be characterized as Mediterranean with the majority of precipitation (yearly average = 132 cm) occurring during winter. Elevational gradients, soil diversity and differences in historic land management practices have resulted in diverse plant communities throughout the area [see Allen et al. (2014) for a detailed description].

The study area supported a diverse predator–prey community although black-tailed deer were the only common ungulate. Tule elk *Cervus elaphus nannodes* and non-native wild pigs *Sus scrofa* were observed during the study but not considered resident. Common predators included pumas *Puma concolor*, black bears *Ursus americanus*, coyotes *Canis latrans* and bobcats *Lynx rufus*. Small mammalian prey species were abundant and ubiquitous and included several lagomorphs (e.g., black-tailed jackrabbits; *Lepus californicus*) and rodents (e.g., California ground squirrels; *Otospermophilus beecheyi*). Black-tailed deer were hunted but only adult males were legally harvestable.

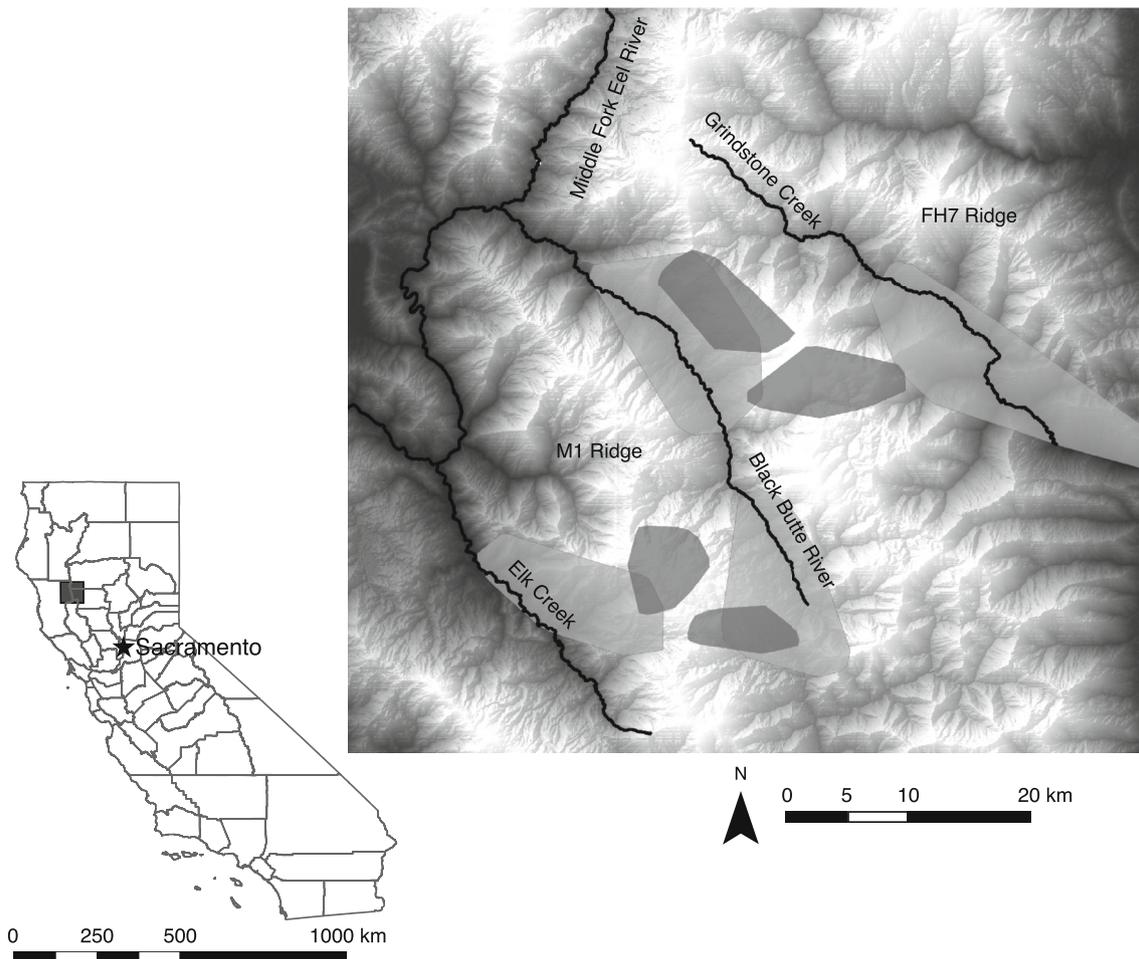


Fig. 1 Study area in the larger context of the State of California, USA. Lighter colours depict high elevations and darker colours low elevations with major ridges and watersheds identified. Low elevation

deer winter ranges (*light grey polygons*) and high elevation summer ranges (*dark grey polygons*) were identified based on telemetry data

Animal captures and monitoring

All handling procedures were approved by an independent Institutional Animal Care and Use Committee at the University of California, Davis (Protocols 15341 and 16886).

Fawns

Between 2009 and 2012 we captured a total of 137 fawns from 4 different cohorts. One fawn died because of capture related injuries and was excluded from all analyses. From mid-June to mid-July of each year, we searched for newborn fawns alongside accessible roads on both the FH7 and M1 ridge and hand-captured them using nets. During night captures we used spotlights to facilitate detection. Capture crews wore gloves during captures to avoid scent contamination, and fawns were immediately transferred into pillowcases scented with native aromatic plants to minimize stress. Fawns were subsequently sexed, weighed,

aged [based on visual evaluation of their standing/walking ability, state of the umbilical cord (wet versus dry) and morphometrical measurements including hoof growth; Sams et al. 1996] and fitted with a coloured ear tag in one ear and a motion-sensitive very high frequency (VHF) ear tag transmitter (Sirtrack, Havelock North, New Zealand) with 1-year battery life in the other ear. Total processing time lasted between 8 and 12 min and fawns were released at their respective capture sites to facilitate reunion with their mothers.

We monitored status of fawns daily from their date of capture through mid-September using ground-based telemetry. Monitoring switched to a 10–14 day interval during the rest of the year and was conducted both from the ground and the air. VHF transmitters were programmed to switch to a mortality signal when they remained stationary for 4 h allowing rapid site investigations to determine fate and cause of mortality. We assigned cause of mortality based on evidence found at the mortality site including

predator tracks and scats, state of remains, evidence of caching, bite marks, and blood.

Adults

Between June 2009 and August 2013 we captured a total of 60 adult female black-tailed deer using free range darting. Three individuals died because of capture related causes and were excluded from all analyses. Captures occurred during summer at high elevations along the 2 main ridges (FH7 and M1) where deer were darted opportunistically from vehicles while driving along unpaved forest roads. Detailed capture and handling procedures including drug dosages are described in Casady and Allen (2013). Once anesthetized, deer were weighed, measured, and one lower canine tooth was extracted for age determination based on cement-annuli methods (Matson's Laboratory LLC, Missoula, MT, USA). We determined if deer were pregnant during capture using 2 different methods. First, we took blood from a sample of individuals ($n = 43$ individuals) and used progesterone levels to determine pregnancy (Wood et al. 1986). Second, we verified if does were lactating or had a fawn at heel during captures and used this information to confirm pregnancy for does captured prior to July 15th of any given year ($n = 4$ individuals). We also used ultrasound and physical examinations on a small number of individuals to determine the number of fetuses in uteri ($n = 11$ individuals). Deer were then fitted with numbered ear tags and motion-sensitive store-on-board GPS collars (models 3300 and 4400 M, Lotek Wireless, Inc., Newmarket, Ontario, Canada and Telonics, Mesa, Arizona, USA) that contained VHF transmitters. Collars ranged in weight and we used lighter models on smaller deer ensuring that collar weights never exceeded 3 % of bodyweight.

Collared does were monitored from the ground at least 2 times per week during the summer months (June–September) when we intensively monitored fawns (see above). During other times of the year, monitoring occurred every 10–14 days from either the ground or the air. If a collar remained stationary for 4 h, it switched to mortality mode and we confirmed fate and identified the likely cause of mortality during subsequent site investigations using methods described above. All collars were fitted with automatic release mechanism programmed to drop-off after a maximum deployment period of 2 years.

Survival and cause-specific mortality analyses

We used CMR models to estimate survival in E-SURGE (Choquet et al. 2009). We conducted survival analyses for fawns and adults separately because of differences in maximum deployment periods between VHF transmitters for fawns (always 1 year) and GPS collars for adults (either 2 years, $n = 32$ or 1 year, $n = 25$). Based on our monitoring schedule we described monthly encounter histories resulting in 48 recapture occasions for fawns and 51 recapture occasions for adults.

For our survival analyses, we extended a multistate CMR model previously described by Schaub and Pradel (2004) to encounter histories typically obtained from telemetry studies. Our models accounted for censored individuals due to collar failures (see below) that are still potentially at risk of mortality because previous research has highlighted the importance of incorporating unobservable states when modelling mortality causes (Tavecchia et al. 2012). Because of rugged terrain resulting in limited access during winter, we could not always verify the status of fawns (see below). We thus accounted for their detection probabilities to more accurately estimate their survival. For adult females, we accounted for the probability of collar failure but set the detection probability to 1 since functioning GPS collars provided consistent and reliable survival data independent of ground monitoring.

Multistate transition matrices

Individuals with known fates were assigned one of the following 3 states for a particular encounter occasion: alive ($A+$), newly dead due to predation ($DP+$), or newly dead due to other, unknown causes ($DO+$). Individuals with unknown fates were assigned one of the following 3 unobservable states: alive ($A-$), newly dead due to predation ($DP-$), or newly dead due to other causes ($DO-$). Individuals dying at time t transitioned into an absorbing state (D) at time $t + 1$ during the recapture occasion independent of cause of mortality (Gauthier and Lebreton 2008). We assigned “unobservable” states to individuals that either dropped their transmitters (1 fawn, 17 adults) or experienced likely equipment failure (4 fawns, 5 adults). Since other mortalities (DO) potentially included predation, the proportion of death caused by predation is likely underestimated. The transition matrix T from state t to another state at time $t + 1$ could then be written as:

$$T = \begin{bmatrix} & A+ & A- & DP+ & DP- & DO+ & DO- & D \\ A+ & \alpha\phi & (1-\alpha)\phi & \alpha(1-\phi)\beta & (1-\alpha)(1-\phi)\beta & \alpha(1-\phi)(1-\beta) & (1-\alpha)(1-\phi)(1-\beta) & 0 \\ A- & 0 & \phi & 0 & (1-\phi)\beta & 0 & (1-\phi)(1-\beta) & 0 \\ DP+ & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DP- & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DO+ & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ DO- & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ D & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

The above matrix T was decomposed into 3 actual transition matrices in E-SURGE. The first matrix allowed estimating α , the probability that a telemetry device functioned up to its expected lifespan. The second matrix allowed estimating the survival process and its associated probability ϕ . The third matrix allowed estimating the probability of mortality caused by predation β (Schaub and Pradel 2004). For the survival analysis of fawns we also estimated the detection probability, which we assumed to be constant to avoid parameter redundancy (Gimenez et al. 2003).

Selecting best-fit survival models

We developed a set of candidate models to test for temporal and spatial variability in survival probabilities of fawns and adults. We compared models using AIC corrected for small sample sizes and selected the best model with the lowest AIC_c value (Burnham and Anderson 2002). For fawns, we independently tested for effects of summer (i.e., the first 3 months of their life) when the majority of mortalities occurred (Forrester and Wittmer, unpublished data), season, and year and trimester (seasonal effects among years) on survival probabilities and mortality due to predation. Since female selection of fawning sites with respect to habitat may affect survival of fawns (e.g., Ballard et al. 2001), we also tested for spatial variation in both fawn survival probabilities and mortality due to predation among fawning areas (i.e., fawns captured on FH7 versus M1 ridges).

For adult females, we compared models with the same temporal and spatial covariates outlined for fawns above. Model parameters, however, differ due to 3 additional sampling occasions compared to fawns. Since previous research on ungulates including mule and black-tailed deer showed variation in survival probabilities among yearlings, prime-aged females and older individuals (i.e., senescence) (Forrester and Wittmer 2013), we further tested for age-

specific variation in survival probabilities. Such a focus also allowed us to test for variability in predation risk among individuals in different age classes and thus its relationship to senescence. To account for individuals transitioning from one age class to the next [i.e., non-breeding yearlings (5 % of our initial sample), prime-aged adults aged between 2 and 7 years old (74 % of our initial sample), and senescent individuals ≥ 8 years old (21 % of our initial sample)], we corrected age of individuals based on time elapsed since first capture (Choquet et al. 2009).

Population growth

We used a post-breeding Lefkovich projection matrix (Caswell 2001) to estimate the asymptotic growth rate of black-tailed deer in our study area. Because many ungulates including black-tailed deer are strongly age-structured, polygenous and iteroparous (e.g., Gaillard et al. 1998; Forrester and Wittmer 2013), we built a female only matrix, structured into 9 age classes with senescent individuals pooled into 1 class. Adult survival was limited to a maximum age of 22 years, which corresponded to the oldest deer observed in our study area (Allen 2014). Age-specific annual survival rates for fawns (ϕ_f), yearlings (ϕ_y), prime-aged (ϕ_a), and senescent individuals (ϕ_s) from the CMR models were used to parameterize the matrix. We assumed that females give birth for the first time on their second birthday and determined reproductive rates r from the mean proportion of females observed pregnant each year (see above) multiplied by the mean number of fawns per female and adjusted by respective age-specific survival probabilities. We estimated reproductive rates of yearlings r_y separately, since previous research on mule deer suggested that pregnancy rates can be lower for this age group (Monteith et al. 2014). Reproductive rates were divided by 2 to reflect per capita number of female fawns (Caswell 2001). The resulting Lefkovich matrix L was thus described as:

$$L = \begin{bmatrix} 0 & r_y & r_a & r_a & r_a & r_a & r_a & r_a & r_s \\ \phi_f & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_y & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_a & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_a & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_a & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_a & \phi_s \end{bmatrix}$$

We used a simulation approach based on Monte Carlo iterations (Alvarez-Buylla and Slatkin 1993) to account for uncertainty in parameter estimates and population growth. We ran 10,000 Monte Carlo iterations using the *rbeta* function (stats v2.15.3 R package) in which survival probabilities were drawn from a beta distribution with parameters calculated in a way that expectation and standard deviations would be equal to annual survival estimates and standard errors obtained from the multistate CMR analysis. Associated variances of survival probabilities were determined based on standard errors and calculated using the delta method (Burnham and Anderson 2002). For each iteration, reproductive rates were drawn from a log-normal distribution using the mean number of pregnant females per year and related standard deviation obtained from our data. We used the R package (*popbio*) (Stubben and Milligan 2007) to determine the mean (\pm SD) asymptotic growth rate calculated from the dominant eigenvalues of the 10,000 matrices generated from the Monte Carlo iterations.

Sensitivity and elasticity analyses

All sensitivity analyses were conducted using the function *vitalsens* in *popbio* v2.4 R package. We estimated first order sensitivities and elasticities to assess contributions of vital rates from our Lefkovitch matrix using standard methods and equations (Caswell 2001). Since sensitivities and elasticities were estimated from results of each of our 10,000 model iterations (see above), we were able to determine variances associated with each estimate.

We then assessed lower-level elasticities (Caswell 2001) to quantify the relative importance of proportional changes in the underlying components associated with survival (e.g., cause specific mortalities associated with survival estimates of different age classes) on population growth (Gervasi et al. 2012). We tested whether elasticity values were robust with respect to our classification of the cause of mortality by (a) assuming that there was no misclassification of causes of mortality; (b) assuming that approximately 80 % of the observed other causes of adult

Table 1 Candidate models explaining survival probabilities (ϕ) of fawns, all accounting for tag retention (α), sources of mortality (β for predation and $1-\beta$ for other cause), and detection probabilities (p)

Model	Number of parameters	AIC _c	Δ AIC _c	AIC _w
$\alpha, \phi(f + trim), \beta(f + sum), p$	24	1,251	0	0.56
$\alpha, \phi(f + trim), \beta(sum), p$	23	1,252	1	0.34
$\alpha, \phi(f + trim), \beta(f + say), p$	27	1,255	4	0.08
$\alpha, \phi(f + trim), \beta(f + trim), p$	38	1,258	7	0.01
$\alpha, \phi(f + trim), \beta(trim), p$	37	1,258	7	0.01
$\alpha, \phi(f \times sum), \beta(f \times sum), p$	15	1,260	9	0
$\alpha, \phi(f + y), \beta(f + trim), p$	26	1,270	19	0
$\alpha, \phi(f + y), \beta(f + y), p$	15	1,292	41	0
$\alpha, \phi(f + s), \beta(f + s), p$	15	1,306	55	0
$\alpha, \phi(f + say), \beta(f + say), p$	16	1,308	57	0
$\alpha, \phi(trim), \beta(trim), p$	36	1,339	88	0
$\alpha, \phi(f), \beta(f), p$	8	1,345	94	0
$\alpha, \phi(f \times trim), \beta(f \times trim), p$	68	1,360	109	0

We considered the following covariates: fawning area (*f*), trimester (*trim* = season across years), season (*s*), summer (*sum* = 3 months periods following birth), summer across years (*say*), and years (*y*). The symbols “+” and “ \times ” represent additive and multiplicative effects between covariates, respectively

mortality were due to predation while simultaneously assuming that approximately 50 % of other causes of fawn mortality were due to predation; and (c) that approximately 80 % of the other unknown causes of fawn mortality were due to predation while assuming that approximately 50 % of other causes of adult mortality were due to predation.

To do so we replaced the proportion of mortalities due to predation β with $\beta + u(1 - \beta)$ where *u* is the probability of misclassifying mortalities due to predation as other mortalities. For instance, in the sensitivity and elasticity analysis based on assumption b described above, the random value of *u* associated with adults was drawn from a uniform distribution ranging from 0.6 to 1 (mean of 0.8) while the random value of *u* associated with fawns ranged from 0 to 1 (mean of 0.5).

Contributions of predation to lower level elasticities were quantified by decomposing the overall survival rate in each age class *i*, *S_i* by the following expression

$$S_i = 1 - MP_i(1 - \alpha x) - MO_i \tag{1}$$

where *MP_i* and *MO_i* represent the mortality rates due to predation and other causes in age class *i*, obtained from the

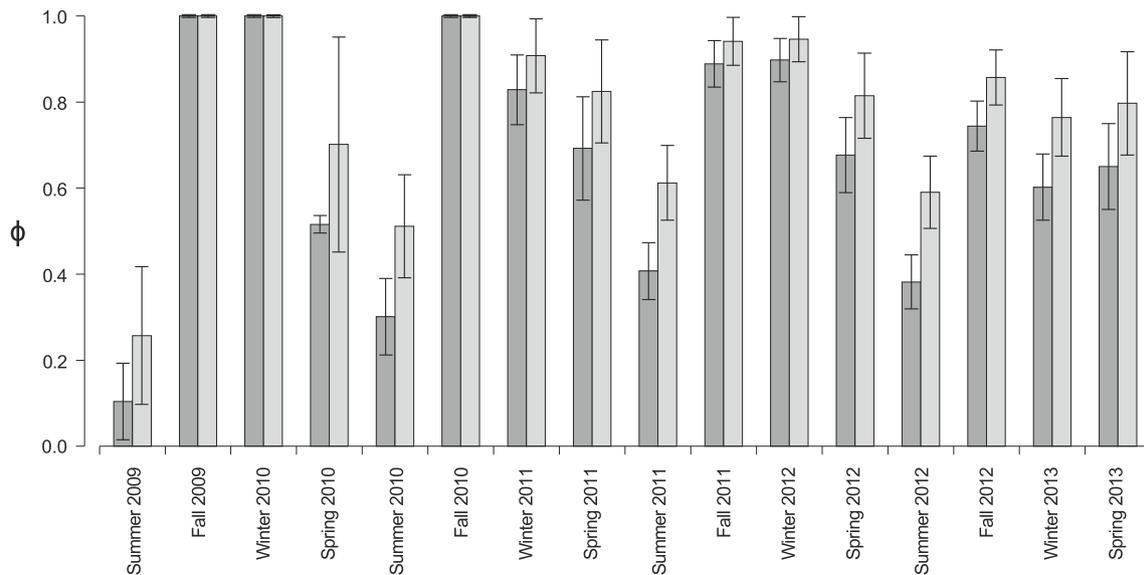


Fig. 2 Survival estimates of fawns <1 years old obtained from the best model including range of seasonal survival probabilities of each year $\phi_{f,s,y}$ across years and among ridges (FH7 = dark grey, M1 = light grey)

Table 2 Parameter estimates based on the best survival model for fawns including range of seasonal survival probabilities of each year $\phi_{f,s,y}$ across years (displayed in Fig. 2) and on both ridges

Parameter	Fawns FH7	Fawns M1
$\alpha = 0.99$ (0)		
$\phi_{f,s,y}$	Range 0.10–0.99 (0.01–0.12)	Range 0.26–0.99 (0.01–0.25)
$\beta_{f,sum}$	0.81 (0.07)	0.78 (0.07)
$\beta_{f,others}$	0.28 (0.10)	0.26 (0.10)
$p = 0.90$ (0.01)		

Probability of death due to predation was consistent across years but varied in summer among fawning area (indicated by the subscript f) and was denoted $\beta_{f,sum}$ in summer and $\beta_{f,others}$ during the rest of the year. Constant probabilities of tag malfunction α and detection p were also estimated. Standard errors (presented in brackets) were calculated using the delta method

product of the CMR estimates $(1 - \phi_i)\beta_i$ and $(1 - \phi_i)(1 - \beta_i)$, with the annual survival probabilities ϕ_i , and the proportion of mortalities due to predation β_i corrected by the probability u of misclassifying mortalities. The parameter a referred to the amount of additive mortality. When a is equal to 1, mortality is fully additive and when it is equal to 0, mortality is compensatory. Finally x_i represents the proportional reduction of mortality due to predation in the case of management action for instance. Multiplying mortality rate due to predation with $(1 - ax)$ then allows evaluating the elasticities of the lower level parameter and thus the demographic outcomes of a management strategy that would reduce mortality by predation (Schaub and Pradel 2004).

Results

Survival and cause-specific fawn mortality

Predation accounted for 69 % of the 93 fawn mortalities we recorded (bears = 29, coyotes = 20, bobcats = 6, pumas = 2, unknown predators = 7). Malnutrition (5 %) and unknown causes other than predation and malnutrition (26 %) accounted for the remaining mortalities.

The best CMR model indicated that survival probabilities varied between the 2 fawning areas and with trimester (i.e., across seasons and years) (Table 1). Seasonal fawn survival on FH7 ranged from 0.10 (± 0.09) to 0.99 (± 0.01) (Fig. 2). Seasonal fawn survival on M1 ranged between 0.26 (± 0.16) and 0.99 (± 0.01). The probability of fawns being killed by predators was higher during summer (0.81 ± 0.07 on FH7 and 0.78 ± 0.07 on M1) than during other seasons (0.28 ± 0.10 on FH7 and 0.26 ± 0.10 on M1) (Table 2). Predation alone was apparently insufficient explaining observed spatiotemporal variability in survival, given that in the second best model ($\Delta AIC_c = 1$) the proportion of death due to predation only varied between summer and the remaining seasons independently of the year and of the fawning area (Table 1).

Survival and cause-specific adult mortality

Predation accounted for 57 % of the 21 adult mortalities we recorded (pumas = 11, bears = 1). Of the remaining mortalities, 10 % were due to poaching and 33 % were due to other, unknown causes.

Table 3 Candidate models explaining survival probabilities (ϕ) of deer >1 year old, all accounting for probability of GPS malfunctioning (α), and sources of mortality (β for predation and $1-\beta$ for other cause) for yearlings, prime-aged adults and senescent individuals

Model	Number of parameters	AIC _c	Δ AIC _c	AIC _w
$\alpha, \phi(a \times trim), \beta(a \times trim)$	105	411	0	0.51
$\alpha, \phi(a + say), \beta(a + say)$	19	412	1	0.30
$\alpha, \phi(a + s), \beta(a + s)$	15	413	2	0.19
$\alpha, \phi(a \times say), \beta(a \times say)$	39	420	9	0
$\alpha, \phi(a + sum), \beta(a + sum)$	11	441	30	0
$\alpha, \phi(a + s), \beta(a + sum)$	13	444	33	0
$\alpha, \phi(a \times s), \beta(a \times s)$	27	445	34	0
$\alpha, \phi(a + trim), \beta(a + trim)$	41	456	45	0
$\alpha, \phi(a + trim), \beta(trim)$	39	465	54	0
$\alpha, \phi(trim), \beta(trim)$	37	467	56	0
$\alpha, \phi(y), \beta(y)$	13	468	57	0
$\alpha, \phi(f + s), \beta(f + s)$	14	469	58	0
$\alpha, \phi(f + y), \beta(f + y)$	14	471	60	0
$\alpha, \phi(s), \beta(s)$	11	472	61	0
$\alpha, \phi(i), \beta(i)$	5	505	94	0
$\alpha, \phi(f + trim), \beta(f + trim)$	39	563	152	0
$\alpha, \phi(f), \beta(f)$	7	580	169	0

Covariates included fawning area (f), age (a), constant effects (i), season (s), and summer (sum). Because this analysis included 3 more sampling occasions than in the fawn analysis, models testing effects of summer across years (say) and trimester ($trim$ = season across years) had more parameters than equivalent models shown in Table 1. Survival estimates were adjusted for battery life span and actual age of individuals. The symbols “+” and “ \times ” represent additive and multiplicative effects between covariates, respectively

The 2 best CMR models included multiplicative effects of age and trimester, and additive effects of age and summer survival across years on both survival and cause-specific mortality probabilities (Table 3). Because not all parameters were identifiable in these models, we estimated age-specific survival probabilities from a plausible model (Δ AIC_c = 2) that accounted for additive effects of season and age. In general, survival probabilities were higher during winter (yearlings = 0.91 ± 0.18 , prime-aged adults = 0.96 ± 0.03 , senescent individuals = 0.91 ± 0.07) than during summer (yearlings = 0.87 ± 0.04 , prime-aged adults = 0.94 ± 0.02 , senescent individuals = 0.87 ± 0.02). Effects of predation were strongly age dependent; the Δ AIC_c of the model ignoring such effects was implausible (i.e., Δ AIC_c > 50) (Table 3). The seasonal proportion of mortalities caused by predation ranged from 0.99 ± 0 to 1 for yearlings, from 0.33 ± 0.28 to

0.84 ± 0.17 for prime-aged adults and from 0.31 ± 0.30 to 0.82 ± 0.22 for senescent individuals (Table 4). Predation was the primary cause of mortality (i.e., $\beta > 0.5$) for all individuals ≥ 1 year old in spring and summer.

Even though both survival and predation parameters were identifiable for all age classes, estimated probabilities of predation of yearlings were high and approaching 1 with associated standard errors of zero [see Electronic Supplementary Material (ESM) S1]. These results suggest that the effect of predation on yearlings could have been overestimated likely as a result of small sample sizes.

Annual vital rates for the Lefkovitch matrix

Pregnancy rates and fecundity

Pregnancy rates averaged 0.87 ± 0.05 across years and pregnant females carried an average of 1.9 fawns. We assumed reduced pregnancy rates of 0.60 for yearlings (i.e., we adjusted pregnancy rates of yearlings based on proportional differences in pregnancy rates between yearlings and older individuals presented in Monteith et al. 2014). Estimated fecundity thus averaged 0.57 for yearlings and 0.83 for prime-aged and senescent females (Table 5). Reproductive rates of yearlings, adults and senescent females used in the post-breeding Lefkovitch matrix were equal to 0.32 (= 0.57×0.56), 0.64 (= 0.83×0.77) and 0.46 (= 0.83×0.55), respectively.

Age-specific survival probabilities

Annual fawn survival averaged 0.24 ± 0.16 across years and fawning area (see ESM S2 for detailed calculations). Age-specific annual survival probabilities for females >1 year of age averaged 0.56 ± 0.18 for yearlings, 0.77 ± 0.13 for prime-aged adults, and 0.55 ± 0.08 for senescent individuals (Table 5).

Cause-specific mortality rates

The annual probability of fawns dying due to predation was 0.47 ± 0.26 (Table 5) (see ESM S2 for detailed calculations). Annual mortality rates due to predation for females >1 year were 0.43 ± 0.17 for yearlings, 0.12 ± 0.07 for prime-aged adults, and 0.23 ± 0.07 for senescent individuals (Table 5) (see ESM S2 for detailed calculations).

Population growth rates and first order sensitivities and elasticities

The estimated asymptotic growth rate of the population was 0.82 (SD = 0.13). Population growth was

Table 4 Parameter estimates for females >1 year of age

Parameter	Yearling	Adult	Senescent
$\alpha = 0.97$ (0.01)			
ϕ			
Summer	0.87 (0.04)	0.94 (0.15)	0.87 (0.02)
Fall	0.83 (0.15)	0.92 (0.03)	0.83 (0.05)
Winter	0.91 (0.18)	0.96 (0.03)	0.91 (0.07)
Spring	0.86 (0.10)	0.92 (0.03)	0.84 (0.06)
Annual survival	$\phi_y = 0.56$ (0.18)	$\phi_a = 0.77$ (0.13)	$\phi_s = 0.55$ (0.08)
β			
Summer	1.00 (1.09E-07)	0.84 (0.17)	0.82 (0.22)
Fall	0.99 (1.09E-07)	0.35 (0.21)	0.31 (0.30)
Winter	0.99 (1.16E-07)	0.33 (0.28)	0.30 (0.18)
Spring	1.00 (2.10E-08)	0.62 (0.24)	0.58 (0.24)
Annual arithmetic mean	0.99 (5.50E-07)	0.54 (0.11)	0.50 (0.12)

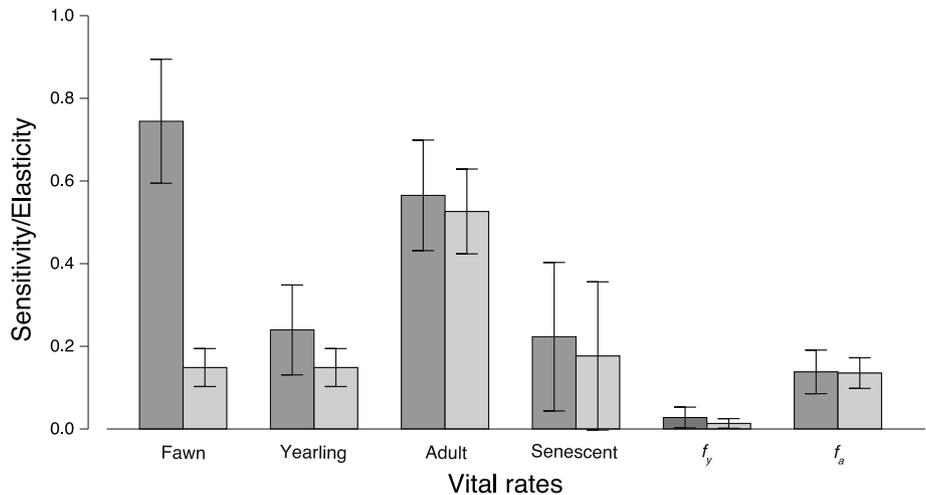
Estimates adjusted for probability of GPS collar malfunction and life expectancy of telemetry devices (α), seasonal and annual survival estimates (ϕ), and probabilities of dying due to predation (β). Standard errors (presented in brackets) are based on seasonal estimates using the delta method. Detection probabilities were constrained to 1

Table 5 Demographic parameters used in the Lefkovitch Matrix including standard errors

Age class	First level analysis	Second level analysis
Fawn	$\phi_f = 0.24$ (0.16)	$MP_f = 0.47$ (0.26) $MO_f = 0.29$ (0.31)
Yearling (1–2 years)	$\phi_y = 0.56$ (0.18)	$MP_y = (1 - 0.56) \times 0.99 = 0.43$ (0.17) $MO_y = 0.04$ (0.01)
Prime-aged (2–7 years)	$\phi_a = 0.77$ (0.13)	$MP_a = (1 - 0.77) \times 0.54 = 0.12$ (0.07) $MO_a = 0.1$ (0.06)
Senescent individual (≥ 8 years)	$\phi_s = 0.55$ (0.08)	$MP_s = (1 - 0.55) \times 0.50 = 0.23$ (0.07) $MO_s = 0.22$ (0.07)
Fecundity		$f_y = 0.60 \times 1.9/2 = 0.57$ (0.04) $f_a = 0.87 \times 1.9/2 = 0.83$ (0.04)

The first order elasticity analysis assessed the contribution of survival to change in growth rate. The lower level elasticity analysis decomposed survival into cause-specific mortality rates (MP for predation and MO for other cause). Standard errors (presented in brackets) are based on seasonal estimates using the delta method. Fecundity remained consistent in both analyses

Fig. 3 First-order sensitivity and elasticity values for vital rates. Mean sensitivities (dark grey) and mean elasticities (light grey) and their 95 % confidence intervals for survival of fawns, yearlings, prime aged adults, senescent individuals, and fecundity of reproductive females (f_y and f_a)



approximately twice as sensitive to changes in survival of prime-aged adults ($E_a = 0.53 \pm 0.01$) than to combined changes in fawn survival, and fecundity of yearlings and adults

($E_f + E_{f_y} + E_{f_a} = 0.15 + 0.01 + 0.13 = 0.29 \pm 0.01$). Among all vital rates, survival of senescent individuals contributed least to population growth (Fig. 3).

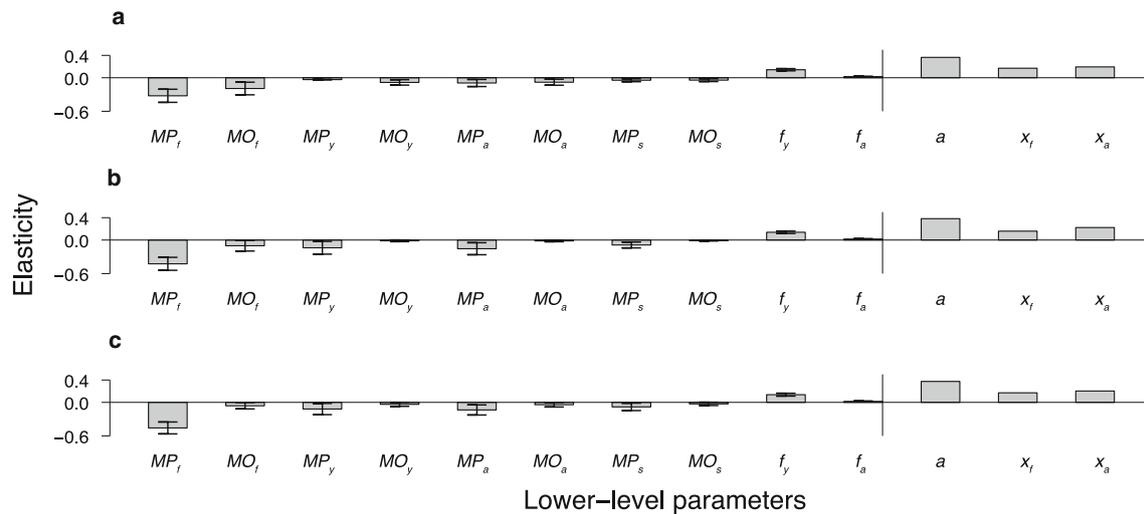


Fig. 4 Lower-level elasticity values and 95 % confidence intervals on the vertical axis. The x axis displays cause-specific mortality rates in each age class [MP and MO defines mortality rates caused by predation and other mortality for fawns (f), yearlings (y), prime aged (a) and senescent individuals (s)] as well as fecundity ($f = f_y + f_a$). To the right of the vertical line are elasticities of lower-level parameters associated with the removal of cause-specific mortalities, assuming mortality by predation is fully additive ($a = 1$), and predation on fawns $x_f = 1$ and on adults $x_a = 1$ is totally removed.

Lower level elasticities and the effect of predation

When decomposing overall survival estimates (Eq. 1) and investigating resulting lower level elasticities, population change was most sensitive to predation of fawns independent of assumed amounts of misclassified mortalities due to predation (Fig. 4). Fawn mortality due to predation continued to have the greatest demographic effect even when pooling elasticities for all 3 adult age classes ($E_{MPf} = 0.38$ versus $E_{MPy} + E_{MPa} + E_{MPs} = 0.25$).

Discussion

Adult female black-tailed deer >1 year of age in our study, a population with a male only harvest, experienced the lowest annual survival rates reported to date in the literature. Based on models that ignored age structure in the population (for comparison with previous studies) but included observed seasonal effects, we found a combined mean annual adult survival rate of 0.71 (± 0.07). This estimate was 15 % lower than the mean annual adult female survival of 0.84 (CV = 0.06) for the species averaged across 21 published studies (reviewed in Forrester and Wittmer 2013). Survival estimates remained very low (mean = 0.77 ± 0.13) even when we only considered survival of prime-aged females between 2 and 7 years of

age. To our knowledge, only 3 previous studies have reported annual adult survival rates of less than 0.80 for mule and black-tailed deer (McNay and Voller 1995; Bleich and Taylor 1998; Robinson et al. 2002). Adult survival did not vary significantly over the 4 years of monitoring. Such consistency is typical for ungulates with similar life histories (Gaillard et al. 1998).

Three scenarios were considered: **a** assuming that there was no misclassification of causes of mortality; **b** assuming that approximately 80 % of the observed other causes of adult mortality were due to predation while simultaneously assuming that approximately 50 % of other causes of fawn mortality were due to predation; and **c** that approximately 80 % of the other causes of fawn mortality were due to predation while assuming that approximately 50 % of other causes of adult mortality were due to predation

Predation accounted for at least 57 % of observed adult mortalities, the majority of which (92 %) were attributed to pumas. Overall, puma predation was the dominant contributor and thus proximate cause of the observed low adult survival including those of prime-aged females. The relative impact of predation was similar to other studies reporting low adult survival for mule and black-tailed deer. However, previous studies identified predation as the primary cause of mortality during winter when adult deer are expected to be in poorer body condition and thus more susceptible to predators (e.g., McNay and Voller 1995; Robinson et al. 2002). Our study suggested greater vulnerability to predation during summer when GPS location data showed that pumas followed migrations of adult deer to high elevation summer ranges (Allen et al. 2014). Structurally diverse habitats on summer ranges may have also increased vulnerability of deer to ambush predators such as pumas (Sih et al. 1998; Pierce et al. 2004). However, differences in monitoring intensity resulted in a greater number of unidentified causes outside the summer

season and thus the potential to underestimate the effect of puma predation during winter.

The observed low adult survival rates due to a specialist predator were unexpected for 2 reasons. First, low adult survival rates in ungulates are not uncommon but more typically reported for rare and endangered species occurring in small populations [e.g., non-migratory woodland caribou *Rangifer tarandus caribou* (Wittmer et al. 2005); bighorn sheep *Ovis canadensis* (Johnson et al. 2010)]. Results from helicopter surveys, however, indicate that black-tailed deer occurred at high densities of approximately 20 individuals/km² at the onset of our study (D. Casady, unpublished data). Second, ungulates and indeed many other species are more likely limited by predation in systems with multiple predator species that are supported by several prey species (see examples of species affected by apparent competition in DeCesare et al. 2010). Black-tailed deer, however, were functionally the sole ungulate in our study area and adult deer were essentially only vulnerable to predation from pumas. One possible explanation for the observed low survival rates is that the deer population may have exceeded its nutritional carrying capacity and animals are taking greater risks to obtain increasingly scarce resources. Another possible explanation for the unsustainable effect of predation on adult deer is that pumas in our study area may have been forced to kill deer more frequently due to high observed rates of usurpation of their kills by black bears during the summer months (Allen 2014). Based on 352 kill site evaluations of 7 GPS collared pumas in our study area, Allen et al. (2014) reported that black-tailed deer contributed 98.6 % to their prey biomass and pumas killed on average 1.07 deer/week. These kill rates are among the highest reported for pumas across their range (Knopff et al. 2010).

Concurrent to low adult survival, black-tailed deer in our study also experienced approximately 17 % lower annual survival of fawns than typically reported (i.e., 0.24 versus 0.29; Forrester and Wittmer 2013). The low fawn survival was primarily a consequence of high predation from a diverse number of predators during summer. Fawn survival was more consistent than generally reported but still exhibited significant spatiotemporal variability over the 4-year duration of our study. For instance, fawn survival varied between ridges (and thus fawning areas). However this variation was apparently independent of differences in predation. Future analyses of the variables affecting fawn survival thus need to evaluate spatial differences in seasonal food availability and yearly variation in climate or litter size to better understand the effect of limiting factors other than predation (White et al. 1987; Lomas and Bender 2007; Johnstone-Yellin et al. 2009).

Given the low survival rates for individuals from all age classes including fawns it is not surprising that the deer

population in the Mendocino National Forest is currently predicted to decline dramatically. The decline is occurring despite relatively high fecundity rates that saw >85 % of adult females older than 2 years pregnant every year. While Forrester and Wittmer (2013) suggested that high fecundity rates enable mule and black-tailed deer to compensate for low fawn survival, the reproductive potential was insufficient to account for the combination of low fawn and adult survival. Such a pattern has been described for many small ungulate populations exhibiting similar rates of decline as those observed in our study and that identified predation as the primary cause of mortality (e.g., Wittmer et al. 2005, 2013; Johnson et al. 2010). The predicted significant negative asymptotic growth associated with high predation rates strongly suggests that top-down effects are responsible for declines. Quantitative analyses of bottom-up effects on mortality as well as estimates of population size and trends, however, are required to understand if predation is limiting or regulating the population (Sinclair and Pech 1996). Furthermore, future analyses need to evaluate if the predicted population decline is part of a multi-decadal cycle hypothesized to occur in mule and black-tailed deer in North America (Leopold et al. 1947; Forrester and Wittmer 2013).

Methodology played a significant role in our ability to quantify top-down effects on survival probabilities and thus population dynamics. In particular, our multistate CMR models enabled us to directly evaluate the effects of spatial, temporal and individual variation associated with a dominant proximate cause of mortality (i.e., predation) and directly quantify its contribution to age-specific survival probabilities. Even though multistate CMR models are often over-parameterized and may thus include redundant parameters (Gimenez et al. 2003), they have important advantages over other currently used survival analyses based on encounter histories of individuals. For example, non-parametric methods such as Kaplan–Meier are commonly used to estimate survival probabilities but lack ability to link resulting estimates to changes in explanatory variables (Heisey and Fuller 1985; Murray 2006). Cox proportional hazard (CPH) models allow examining the relative effect of changes in covariates on the instantaneous risk of death while a baseline hazard function changes over time (Hebblewhite and Merrill 2011; DeCesare et al. 2014). However, because CPH models are semi-parametric, the effects of covariates can be misinterpreted if a) assumptions of the baseline hazard functions are violated, and b) important information remains ‘hidden’ in said baseline hazard functions (Murray 2006). Nevertheless, CPH models are a powerful tool to model the continuous mortality risk associated with time dependent covariates, group stratification and random effects (Murray 2006), and may be better suited for studies attempting to investigate the role of multiple environmental variables on survival probabilities in more

complex systems where proximate and ultimate causes of mortality differ (DeCesare et al. 2014).

Perhaps the greatest advantage of directly decomposing the effect of predation on age-specific survival estimates became apparent when we incorporated said estimates into lower level elasticity analyses (see also Gervasi et al. 2012 for an example involving roe deer *Capreolus capreolus*). In particular, results from our standard first-level sensitivity analysis confirmed the overall importance of adult survival in influencing population dynamics of ungulates (Gaillard et al. 2000). In contrast, results from our lower-level elasticity analysis suggested that any variation in fawn mortality due to predation from 4 different predator species would have the greatest effect on population growth. This result is interesting from a theoretical perspective for at least 3 reasons. First, because our survival analyses revealed temporal variation in fawn survival, population dynamics (i.e., changes in λ) were most sensitive to the low observed adult survival rates. However, because predators killed fawns at consistently high rates over time, it was the combined effect of multiple predators on fawns that contributed disproportionately to overall fitness as predicted by the canalization theory (Gaillard and Yoccoz 2003). Second, predator species primarily preying on fawns in our study were generalists or depending on species other than deer (i.e., their numbers were likely facilitated by alternate prey species) (Wilmers et al. 2007; Prugh et al. 2009). This opens the possibility of deer in our study area being subjected to apparent competition (Holt and Lawton 1994). Third, mule and black-tailed deer are believed to have evolved under selective pressure from specialist ambush predators particularly pumas (Laundré 2010). Since pumas, however, primarily rely on killing adult deer (Ballard et al. 2001) our findings highlight the possibility of an inability of mule and black-tailed deer to reconcile opposing selection pressures from predators targeting adults versus predators targeting fawns (Sih et al. 1998).

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