Mountain goat survival and mortality during a period of increased puma abundance in the Black Hills, South Dakota

Chadwick P. Lehman¹, Eric M. Rominger² and Brady Y. Neiles¹

¹South Dakota Department of Game, Fish, and Parks, Custer, SD, United States of America
²New Mexico Department of Game and Fish, Santa Fe, NM, United States of America

ABSTRACT

We investigated survival and cause-specific mortality for a mountain goat (Oreamnos americanus) population during a period when the puma (Puma concolor) population was growing in the Black Hills, South Dakota, 2006–2018. We obtained survival data from 47 adult goats (n = 33 females, n = 14 males). Annual survival varied from 0.538 (95% CI [0.285–0.773]) to 1.00 (95% CI [1.00–1.00]) and puma predation was the primary cause-specific mortality factor over a 12-year period. Cumulative hectares of mountain pine beetle (Dendroctonus ponderosae) disturbance was a covariate of importance (wᵢ = 0.972; β = 0.580, 95% CI [0.302–0.859]) influencing survival. To our knowledge, this is the first account of puma being the primary mortality factor of mountain goats over a long-term study. The Black Hills system is unique because we could examine the expanded realized niche of puma in the absence of other large carnivores and their influence on mountain goats. We hypothesize that puma were being sustained at higher densities due to alternate prey sources (e.g., white-tailed deer; Odocoileus virginianus) and this small population of mountain goats was susceptible to predation by one or several specialized puma in the Black Hills. However, we also hypothesize a changing landscape with increased tree mortality due to insect infestation provided conditions for better predator detection by goats and increased survival. Alternatively, open canopy conditions may have increased understory forage production potentially increasing mountain goat survival but we did not evaluate this relationship. Survival and mortality rates of mountain goats should continue to be monitored as this small population may be highly susceptible to population declines due to slow growth rates.

INTRODUCTION

Dynamics of ungulate-predator systems can be difficult to disentangle because of the confounding effects of weather, alternate prey sources, and the interactions of multiple predator species (Bergerud & Ballard, 1988; Boutin, 1992; Rominger et al., 2004; Festa-Bianchet & Côté, 2008). Predator populations can facilitate ecosystem change by altering
abundance or behavior of prey (Schmitz et al., 2008). In some cases, the reduction or extinction of one prey species may be controlled by a predator that is augmented by an abundant, alternate prey species (DeCesare et al., 2010). In ecological theory ‘apparent competition’ is the indirect interaction between (at least) two prey species and a shared predator (Holt, 1977). A decline in one species may coincide with an increase in the other and the conservation of large mammals depends on our understanding this interaction in small populations (Morris & Doak, 2002). Unfortunately, there is little information on the unpredictable nature of predation by individual specialist predators on small ungulate populations (Vazquez-Domínguez, Ceballos & Cruzado, 2004; Festa-Bianchet et al., 2006). Whether it be by a specialist predator, or by apparent competition with increased alternate prey, some isolated or endangered ungulate populations have been unable to recover (Festa-Bianchet, 1991; Kinley & Apps, 2001; Festa-Bianchet et al., 2006).

The dynamics of predator–prey ecology as it pertains to mountain goats (Oreamnos americanus) is very different from most mountain ungulate populations because their generally small population size does not provide a sufficient prey base to sustain most predators (Festa-Bianchet & Côté, 2008). Mountain goats rely on precipitous escape terrain to minimize predation risk and in the Black Hills rugged habitats are typically granite outcroppings (South Dakota Department of Game, Fish and Parks, 2018). Unlike cervids, their affinity for using precipitous escape terrain makes it much more difficult for coursing predators to prey upon them, so a specialized hunting technique would be required (Côté & Festa-Bianchet, 2003). A stalking predator such as puma (Puma concolor) could become an effective predator of mountain goats, particularly if mountain goats are predictable in using habitats where they are more vulnerable over time (Festa-Bianchet & Côté, 2008). A few specialized predators could have a substantial impact on small mountain goat populations because they are vulnerable to decline because of their low rates of population recruitment (Bailey, 1991; Festa-Bianchet, Urquhart & Smith, 1994). Most mountain goat populations are too small to provide a prey base for a population of predators, and a single puma that specialized on preying on mountain goats could have a strong influence on a local herd (Côté & Festa-Bianchet, 2003). Therefore, it has been hypothesized that such effects of predation on mountain goat population dynamics may be density independent (Côté & Festa-Bianchet, 2003).

Predation on mountain ungulates, hypothetically, has been influenced by a change in the apex predator guild following the extirpation of wolves (Canis lupus) and grizzly bears (Ursus arctos) in many areas of their former native range (Rominger, 2018). Following the extirpation of wolves in the western United States in the early 1900’s, the formerly subordinate puma became the dominant predator of mountain ungulates in many ecosystems (Boyd & Neale, 1992; Kortello, Hurd & Murray, 2007; Ruth et al., 2011; Elbroch et al., 2015). Puma have been documented as the primary predator of ungulates including mule deer (Odocoileus hemionus) (Logan & Sweanor, 2001), elk (Cervus elaphus) (Rearden, Anthony & Johnson, 2011; Lehman, Rota & Millsbaugh, 2017a), woodland caribou (Rangifer tarandus) (Kinley & Apps, 2001), and bighorn sheep (Ovis canadensis) (Rominger & Weisenberger, 2000; Rominger et al., 2004). The ecological shift of the apex predator guild from a coursing Canid predator to a stalking Felid predator has contributed to the decline
of some ungulate populations such as woodland caribou (Compton, Zager & Servheen, 1995), Sierra Nevada bighorn sheep (Wehausen, 1996), and New Mexico desert bighorn sheep (Goldstein & Rominger, 2012). The ability of puma to prey switch from more numerous sympatric ungulates, primarily deer (Odocoileus spp.) or domestic cattle (Bos Taurus), contributes to declining populations of the more rare ungulate (Lehman, Rota & Millspaugh, 2017a; Rominger, 2018). It is hypothesized that many mountain ungulates have fallen into an ecological trap following the expansion of the realized niche of pumas (Hutchinson, 1957; Dwernychuk & Boag, 1972; Rominger, 2018). The current facilitation of wolf and grizzly bear recovery may have profound effects on the persistence of puma and its role as a dominant predator in some mountain ungulate communities.

Puma need to stalk within a short distance from prey in order to make a successful kill; dense vegetation is often used to cover their approach before attacking (Logan & Irwin, 1985; Koehler & Hornocker, 1991; Laundre & Hernandez, 2003; Lehman et al., 2017b). Transition zones from cover or escape terrain areas to foraging areas have been hypothesized to provide areas where puma may have greater success of killing prey (Laundre & Hernandez, 2003). When mountain goats cross transition zones that are heavily forested they may be highly susceptible to puma predation (Côté & Festa-Bianchet, 2003; Laundre & Hernandez, 2003). It has been hypothesized that risk of predation by puma on mountain goats is higher in areas with trees which provide cover for ambush predators (Côté & Beaudoin, 1997; Côté & Festa-Bianchet, 2003).

Mountain goats were introduced into the Black Hills in 1924 and this heavily forested system is unlike the open alpine habitats typical of their native range (South Dakota Department of Game, Fish and Parks, 2018). Surveys indicated our study population to be small and slow growing from 2000–2018. Mountain goat counts have varied from a high of ∼130 in 2016–18 to < 60 in 2009–11 with an average annual growth rate of 1.02 (95% CI [0.88–1.16]) (South Dakota Department of Game, Fish and Parks, 2018). Managers have struggled to understand the potential causes for this population’s limited population growth, but a hypothesis is that mountain goats may have fallen into an ecological trap by puma predation in the Black Hills. Both wolves and grizzly bears were extirpated from the Black Hills allowing the once subdominant puma to become dominant (Mattson & Merrill, 2002; Ripple, Wirsing & Letnic, 2013). We also hypothesize that the unique vegetation conditions of the Black Hills may impede the ability of mountain goats to detect predators because dense ponderosa pine (Pinus ponderosa) stands reduce visibility while also providing stalking cover for puma. The Black Hills offered a unique opportunity to examine mountain goat survival and mortality in a system dominated by a single large carnivore. Our primary objectives were to: (1) determine annual survival rates of mountain goats; and (2) quantify cause-specific mortality.

**MATERIALS & METHODS**

**Study Area**

The study area was located in Custer, Pennington, and Lawrence counties spanning the Black Hills, South Dakota, USA (Flint, 1955) and was primarily public land (Fig. 1).
Elevation ranges from 1,186 m to 2,208 m above mean sea level. Mean annual precipitation ranged from 52–54 cm and mean annual temperature ranged from 6–9 °C across the study area (National Climatic Data Center, 2015). Forests were dominated by ponderosa pine and some high elevation areas also had intermixed spruce (Picea glauca) and aspen (Populus tremuloides; (Larson & Johnson, 1999). Precipitous terrain included granite outcroppings and these geologic features occurred primarily near the highest elevation of Black Elk Peak (Redden, Norton & McLaughlin, 1982). Potential nonhuman predators of mountain goats included puma, bobcats (Lynx rufus), and coyotes (Canis latrans).

Capture and handling
We radiomarked study animals from a small population of mountain goats which ranged in size from approximately 50–130 animals (Table 1). We captured adult mountain goats (≥3 years of age) using net-guns fired from helicopters and from the ground (Cadsand, Jex & Gillingham, 2010); we also captured mountain goats using clover traps baited with salt during October through March 2000–2016 (Clover, 1956; Cadsand, Jex & Gillingham, 2010). We fitted captured goats with very high frequency (VHF) telemetry collars (Telonics, Mesa, AZ, USA; Advanced Telemetry Systems, Isanti, MN, USA). Captured goats were aged by counting horn annuli (Brandborg, 1955; Stevens & Houston, 1989). We subsequently classified individuals into 2 a priori age classifications chosen to correspond with stages of senescence and producing young (Côté & Festa-Bianchet, 2003; White et al., 2011). We classified goats as adult (3–9 yrs) and old adult (10+ yrs). We did not mark any goats that were yearling or 2 years old (i.e., subadult) so we only evaluated 2 age classes. We monitored most individuals over multiple years. All handling, marking, and monitoring procedures were approved by the South Dakota Department of Game, Fish, and Parks (Permit Numbers 1–3).

Survival and mortality
We used daily survival analysis (Nest Survival Module in Program MARK, version 9.0; White & Burnham, 1999; Cooch & White, 2009) via RMark (Laake, 2013) in Program R (Team, 2019) to examine specific hypotheses regarding how age, gender, and mountain pine beetle disturbance influenced mountain goat survival. This approach uses generalized linear modeling with the use of the logit link function as it is the natural link for the binomial distribution (McCullagh & Nelder, 1989; Rotella, Dinsmore & Shaffer, 2004). We hypothesized that old age can negatively influence survival, particularly when goats are ≥10 years of age (Festa-Bianchet & Côté, 2008). We hypothesized that males will have poorer survival than females (Festa-Bianchet & Côté, 2008). It has been hypothesized that risk of predation by puma on mountain goats is higher in areas with trees which provide cover for ambush predators (Côté & Beaudoin, 1997; Côté & Festa-Bianchet, 2003). We hypothesize that cumulative hectares of mountain pine beetle (Dendroctonus ponderosae) disturbance will create more open conditions for mountain goats to visually detect predators (see description of how we developed this covariate below). We ranked our competing models using Akaike’s Information Criterion (Burnham & Anderson, 2002). We considered models differing by ≤2 AICc as alternatives to the selected model but preferred the simplest model.
Figure 1  The Black Hills, South Dakota study area where we studied mountain goats, 2006–2018. We provide the spatial distribution of goats using locations with 99% Brownian bridge movement model contours.

We based our conclusions on parameter estimates from the best model. Telemetry on individuals was conducted 2–3 times weekly to determine survival status (Broecher, 2013). We evaluated annual periods of survival based on the biological period of when most mountain goats are born, which occurs from 1 June–31 May of each year (White et al., 2011). Once a mortality signal was detected we determined cause-specific mortality of goats immediately using several diagnostics. We necropsied the carcass immediately
and scrutinized mortality sites for predator sign. We classified cause of mortality as: (1) predation when evidence at the mortality site indicated that the goat had been alive when attacked (e.g., hemorrhaging); (2) fall; (3) drowning; and (4) unknown if the cause of mortality could not be determined. We further assigned predation-caused mortalities to species of predator based on characteristics of predator kills (O’Gara, 1978). We investigated the area for cache sign, drag marks, scat, and hair (Lehman, Rota & Millspaugh, 2017a). We necropsied goat remains, looking for signs of hemorrhaging and bite marks, and measured bite marks to the nearest mm.

We estimated cause-specific mortality rates using cumulative incidence functions (CIF; (Heisey & Patterson, 2006). We used the “mort” package of Program R (Sargeant, 2020) to estimate CIFs, which allowed the estimation of cause-specific mortality in the presence of competing mortality factors (Heisey & Patterson, 2006). Competing factors occur when an animal is exposed to ≥1 potential cause of mortality, and the incidence of one event prevents others from occurring.

**Evaluation of habitat change**

We first estimated 99% contour home ranges with Brownian bridge movement models (BBMMs), using a 50 m grid size (Horne et al., 2007), implemented with the ‘BBMM’ package (Nielson, Sawyer & McDonald, 2014) in program R (ver. 3.3.2, 2019, <http://www.r-project.org >) with VHF transmitters that were visually located 2–3 times weekly. We estimated home ranges annually from 1 June–31 May (Fig. 1). We then overlaid the 99% contours with the Black Hills National Forest (BHNF) Forest Service Vegetation (FSVEG) GIS coverage (BHNF, unpublished data) of mountain pine beetle infested trees. This coverage was developed using a combination of aerial surveys, NAIP data, and aerial photographs that were digitized into ArcGIS from 2006–2018 (Backsen & Howell, 2013). Cumulative hectares of mountain pine beetle disturbance was used as a covariate in mountain goat survival.

**Abundance estimates**

We obtained abundance estimates of mountain goats using helicopter surveys. A sightability model was used to estimate population size using radio-collars and the mean detection rate from several flights conducted from 2006–2013; from 2014–2018, a Poisson log-normal mark-resight estimate was used to estimate population size from radio-collared mountain goats in 2-year intervals (Broecher 2013, South Dakota Department of Game, Fish and Parks, 2018). Abundance estimates occurred in the core area of the mountain goat range (South Dakota Department of Game, Fish and Parks, 2018). We obtained abundance estimates of puma (which includes kittens) using the Lincoln-Peterson method with radiomarked or DNA marked individuals and hunter harvest; abundance estimates occurred within the Black Hills Fire Protection District (South Dakota Department of Game, Fish and Parks, 2019).

**RESULTS**

We obtained survival data from 47 adult (≥3 years of age) individuals (n = 33 females, n = 14 males). Pooled annual survival probability varied from 0.538 (95% CI [0.285–0.773])
Table 1  Abundance* estimates of mountain goats in the Black Hills, South Dakota 2006–2018.

| Year | Abundance estimate | 95% CI |
|------|-------------------|--------|
| 2006 | 70                | [61, 79] |
| 2007 | 62                | [53, 71] |
| 2008 | 71                | [60, 81] |
| 2009 | 56                | [48, 65] |
| 2010 | 76                | [64, 88] |
| 2011 | 55                | [46, 63] |
| 2012 | 104               | [89, 120] |
| 2013 | 111               | [95, 127] |
| 2014 | 121               | [99, 207] |
| 2016 | 133               | [106, 236] |
| 2018 | 135               | [95, 373] |

Notes.
*Using helicopters, a sightability model was used to estimate population size using radio-collars and the mean detection rate from several flights conducted from 2006–2013. Using helicopters from 2014–2018, a Poisson log-normal mark–resight estimate was used to estimate population size from radio-marked mountain goats in 2-year intervals. Abundance estimates occurred in the core area of the mountain goat range.

Table 2  Apparent annual survival probability of mountain goats in the Black Hills, South Dakota 2006–2018.

| Year | n  | Survival | 95% CI     |
|------|----|----------|------------|
| 2006 | 18 | 0.652    | [0.360, 0.862] |
| 2007 | 15 | 0.538    | [0.285, 0.773] |
| 2008 | 13 | 0.925    | [0.618, 0.990] |
| 2009 | 17 | 1.000    | [1.000, 1.000] |
| 2010 | 17 | 0.821    | [0.569, 0.941] |
| 2011 | 14 | 0.925    | [0.615, 0.990] |
| 2012 | 12 | 1.000    | [1.000, 1.000] |
| 2013 | 15 | 1.000    | [1.000, 1.000] |
| 2014 | 15 | 1.000    | [1.000, 1.000] |
| 2015 | 15 | 0.934    | [0.652, 0.991] |
| 2016 | 14 | 1.000    | [1.000, 1.000] |
| 2017 | 14 | 0.927    | [0.622, 0.990] |
| 2018 | 13 | 1.000    | [1.000, 1.000] |

Mean annual survival was 0.902 (95% CI [0.825–0.979]) from 2006–18. Puma predation was the largest percentage of cause specific mortality (n = 8 of 17; Table 3). In 2007, during a year of low mountain goat abundance (n = ~50–70) and poor survival (0.538), puma predation (0.289) was the leading cause of mortality for radio-marked mountain goats. The puma population increased substantially from 2006 to 2012 in the Black Hills and has remained relatively stable through 2018 (Table 4).

The top-ranked model explaining annual mountain goat survival included cumulative hectares of mountain pine beetle disturbance (β = 0.580, 95% CI [0.302–0.859]; Table 5). Cumulative hectares of mountain pine beetle tree mortality had a positive relationship
Table 3  Estimates of annual mortality rates with 95% confidence intervals and number of deaths observed (n) for mountain goats monitored in the Black Hills, South Dakota 2006–2018. Years not listed below had annual survival of 1.0 with no mortalities.

| Year | Mortality factor | n | Mortality rate* | 95% CI     |
|------|------------------|---|-----------------|------------|
| 2006 | Puma             | 1 | 0.071           | [0.000, 0.197] |
|      | Old age          | 1 | 0.077           | [0.000, 0.211] |
|      | Fall             | 1 | 0.125           | [0.000, 0.327] |
|      | Drowning         | 1 | 0.077           | [0.000, 0.211] |
| 2007 | Puma             | 4 | 0.289           | [0.052, 0.495] |
|      | Unknown          | 2 | 0.175           | [0.000, 0.369] |
| 2008 | Unknown          | 1 | 0.077           | [0.000, 0.211] |
| 2010 | Puma             | 2 | 0.118           | [0.000, 0.258] |
|      | Fence            | 1 | 0.059           | [0.000, 0.164] |
| 2011 | Fence            | 1 | 0.071           | [0.000, 0.197] |
| 2015 | Puma             | 1 | 0.067           | [0.000, 0.185] |
| 2017 | Unknown          | 1 | 0.071           | [0.000, 0.197] |

Notes.
*We estimated cause-specific mortality using cumulative incidence functions (CIF; Heisey & Patterson, 2006).

on mountain goat survival (Fig. 2). Other model coefficients from competing models evaluated included age class (β = 0.333, 95% CI [−0.772–1.439]), gender (β = 0.471, 95% CI [−0.585–1.526]), and year (12 different β coefficients and all of the CIs overlapped 0).

DISCUSSION

Collecting demographic data and using marked individuals of known age is important for assessing population dynamics of long-lived species (Oli, 2003); however, such information is rarely available (Hamel, Côté & Festa-Bianchet, 2006). Population dynamics of mountain goats are poorly understood and vary greatly across their range (Festa-Bianchet, Urquhart & Smith, 1994; Côté & Festa-Bianchet, 2003). Sensitivity analysis indicated survival of adult females is very important for population growth of mountain goats, particularly for older aged females (5+ years and older; Hamel, Côté & Festa-Bianchet, 2006). In our study, survival estimates were lower from 2006–2010 (0.79) and improved during 2011–2018 (0.97) with overall average survival (0.90) being similar to that reported for annual survival of adult females (≥2 years of age) across their range (Smith, 1986a; Festa-Bianchet and Côté, 2008).
Table 4  Abundance estimates\(^a\) and harvest of puma in the Black Hills, South Dakota 2006–2018.

| Year | Abundance estimate | Abundance method | 95% CI | Harvest (n) |
|------|--------------------|-----------------|-------|------------|
| 2006 | 135                | Radiomarked     | [90, 180] | 13         |
| 2007 | 155                | Radiomarked     | [113, 197] | 15         |
| 2008 | 386                | Radiomarked     | [223, 549] | 17         |
| 2009 | 200                | Radiomarked     | [149, 251] | 26         |
| 2010 | 259                | Radiomarked     | [161, 359] | 40         |
| 2011 | 395                | Radiomarked     | [154, 639] | 47         |
| 2012 | 314                | Radiomarked     | [179, 450] | 73         |
| 2013 | 229                | Radiomarked     | [154, 305] | 61         |
| 2014 | 276                | DNA             | [146, 411] | 53         |
| 2015 | 245                | DNA             | [131, 365] | 43         |
| 2016 | 260                | DNA             | [138, 390] | 41         |
| 2017 | 300                | DNA             | [114, 495] | 30         |
| 2018 | 532                | DNA             | [111, 970] | 31         |

Notes.  
\(^a\)Puma abundance, which includes kittens, was estimated using the Lincoln-Peterson method with radiomarked or DNA marked individuals and hunter harvest. Abundance estimates occurred within the Black Hills Fire Protection District.

Table 5  Results of model selection for survival of mountain goats in the Black Hills, South Dakota 2006–2018. Competing models included the covariates age class, gender, year, and cumulative hectares of mountain pine beetle disturbance (beetle).

| Survival Models | AIC\(_c\) | \(\Delta\)AIC | K | \(w_j\) |
|-----------------|-----------|---------------|---|--------|
| Beetle\(^a\)    | 296.370   | 0.000         | 2 | 0.951  |
| Year            | 303.515   | 7.145         | 13| 0.027  |
| Age class\(^b\) + beetle\(^a\) + year | 304.949 | 8.579 | 15 | 0.013 |
| Gender + age class + beetle\(^a\) + year | 306.820 | 10.450 | 16 | 0.005 |
| Gender + beetle\(^a\) + year | 307.276 | 10.906 | 15 | 0.004 |
| Intercept model | 314.726   | 18.356        | 1 | <0.001 |
| Gender          | 315.993   | 19.624        | 2 | <0.001 |
| Age class\(^b\) | 316.390   | 20.020        | 2 | <0.001 |

Notes.  
\(^a\)Cumulative hectares of mountain pine beetle disturbance found within 99% Brownian bridge movement model home ranges of mountain goats.  
\(^b\)Age classes were adult (3–9 years old) and old adult (\(\geq 10\) years old).

In the absence of other large carnivores, puma predation was the dominant source of mortality on mountain goats in the Black Hills. To our knowledge this is the first account of puma being the primary mortality factor of mountain goats over a long-term study. From 2006–2010 the Black Hills mountain goat population may have been in an ecological trap where adaptations derived over time were no longer adaptive. Our case study is similar to other systems where a mountain goat population is too low to provide a consistent prey base for a population of predators, and a single puma that specialized on preying on mountain goats could have a strong impact on a local herd (Côté & Festa-Bianchet, 2003). It has been hypothesized that such predation on mountain goat population dynamics may be density independent (Côté & Festa-Bianchet, 2003). In Alberta, with a more complex...
Apex predator guild, wolves and grizzly bears were 79% of the cause-specific predation mortality of mountain goats, whereas puma were subdominant at 21% of the predation mortality Festa-Bianchet & Côté (2008).

Following the introduction of mountain goats in the early 1920s predation was limited to bobcats and coyotes which are considered inconsequential predators of mountain goats. However, after decades of protection and apex predator management programs in North America, puma have successfully recovered from near extirpation in the early 1900s, leading to reestablishment in many areas including the Black Hills (Berger & Wehausen, 1991; Boyce & Byrne, 2009). Since being listed as a South Dakota state-threatened species in 1978, pumas have increased substantially and the first hunting season of puma occurred in 2005 (South Dakota Department of Game, Fish and Parks, 2019). During 2000-01 mountain goats were certainly exposed to a large stalking carnivore capable of specialized predation in precipitous terrain as visual observations of puma were being reported in the Black Elk Peak area.

Simultaneous with the puma increase, the Black Hills was also undergoing a habitat change of increased ponderosa pine tree density leading to less visibility near escape terrain up until 2006 (Sheperd & Battaglia, 2002; Battaglia, Smith & Sheperd, 2008). Risk of predation by puma is hypothesized to be higher in areas with trees which provide cover for ambush predators (Festa-Bianchet, Urquhart & Smith, 1994; Côté & Beaudoin, 1997). When moving between areas of escape terrain through transition zones that are heavily forested, mountain goats normally use traditional and well-marked trails and often run through areas that are heavily forested (Côté & Festa-Bianchet, 2003). A study of kill sites indicated greater density of trees led to increased susceptibility of elk to puma predation in the Black Hills (Lehman et al., 2017b).
Vegetation conditions changed following a mountain pine beetle epidemic that peaked in the Black Hills in 2012 (Graham et al., 2016). From 2006 to 2012 86% of the mountain goat range had been impacted by mountain pine beetle disturbance causing substantial tree mortality (K Allen, 2016, pers. comm.). Annual survival of mountain goats increased to ≥0.97 following the beetle epidemic from 2011–2018. We hypothesize that the beetle epidemic increased the ability of mountain goats to detect predators due to the increased visibility provided by a reduction in tree cover, particularly in the travel corridors between granite outcroppings where previously dense stands of ponderosa pine were now dead.

It has been hypothesized that an increasing, inversely density dependent predation rate could occur, given a declining prey population and a stable puma population (Rominger et al., 2004; DeCesare et al., 2010; Lehman, Rota & Millspaugh, 2017a). These effects may manifest given the ability of puma to readily switch to alternate prey, ultimately subsidizing the puma population (Rominger et al., 2004; DeCesare et al., 2010). We hypothesize that in the Black Hills, mountain goat abundance did not increase in part because the puma population has been sustained by white-tailed deer (Odocoileus virginianus) as primary prey (Lehman, Rota & Millspaugh, 2017a). White-tailed deer are abundant in our study area at a population estimate of ~51,000 individuals in 2016 (South Dakota Department of Game, Fish and Parks, 2017). A study of puma diets in the Black Hills indicated deer (Odocoileus spp.) comprised the majority of puma diets (83%), and white-tailed deer were the dominant species (63% of total diet; Smith, 2014). Similar patterns of elevated puma predation on less abundant woodland caribou (Rangifer tarandus caribou) and mule deer (O. heminous) were observed in areas with abundant sympatric white-tailed deer (Kinley & Apps, 2001; Robinson, Wielgus & Gwilliam, 2002).

Additional factors may also explain low abundance and slow population growth for this population. Late primiparity by females (i.e., mean age for producing kids starts at 4.9 years) and low recruitment (Adams & Bailey, 1982; Swenson, 1985; Smith, 1986b; Festa-Bianchet, Urquhart & Smith, 1994; Côté & Festa-Bianchet, 2001) characterize mountain goat reproduction. Survival of kids can provide some recruitment to one year of age (>55%; Smith, 1976; Festa-Bianchet & Côté, 2008) but there are very few 4+ year old individual females having kids from year to year due to small population size.

Our results of older aged goats (≥10 years of age) and males not having decreased survival contradicts previous research (Festa-Bianchet & Côté, 2008; White et al., 2011) which could be the result of small sample sizes evaluated for both. Further, our statistical analysis was limited by not evaluating potential random effects associated with years and individuals.

Although most western wildlife management agencies conduct predator control to protect ungulate populations this remains controversial (Reiter, Brunson & Schmidt, 1999). Predator removal is controversial and may only have short-term benefits for ungulate recovery (Reiter, Brunson & Schmidt, 1999; Hurley et al., 2011). Long-term solutions may include reductions of primary prey, which may benefit a rare or declining species by reducing limitation from puma. This was observed on the Patagonian steppe where the native guanaco (Lama guanicoe) increased when alternate prey (i.e., domestic sheep) were reduced in some areas (Novaro & Walker, 2005). In British Columbia, the reduction of
the primary prey source of moose (*Alces alces*) through increased harvest in turn reduced the wolf population stopping the decline of an endangered woodland caribou population (*Serrouya et al., 2017*). Reducing the white-tailed deer population in areas near the core range of mountain goats may benefit this population in the long-term if puma remain the dominant predator in the Black Hills system. Additionally, vegetation management maintaining reduced tree density may decrease puma hiding cover (*Lehman et al., 2017b*) and reducing the amount of vegetation adjacent to precipitous escape terrain may allow mountain goats to better detect predators along movement corridors.

**CONCLUSIONS**

Mountain goats can be highly susceptible to specialized predation when in small populations such as occurs in the Black Hills. A similar phenomena was observed for bighorn sheep in Alberta where the duration of predation events were stochastic and consistent with predation by specialist individuals (*Festa-Bianchet et al., 2006*); bighorn populations experienced one or two distinct puma predation events leading to population declines. Our research highlights the need for long-term studies of survival with a small, slow growing population as annual survival varied greatly over a 12-year period. If our research would have been conducted during shorter time periods (i.e., 2006–2010 or from 2011–2018) we would be reporting a much different result and associated inferences. It is difficult to disentangle the factors of puma predation and changing vegetation conditions in this system. Alternative hypotheses should be considered such as the potential for increased understory forage production potentially increasing mountain goat survival. Future research could continue to evaluate this relationship as ponderosa pine regeneration will presumably continue to increase woody vegetation density following the mountain pine beetle epidemic in the primary mountain goat range of the Black Hills. Additionally, monitoring the dynamics of puma predation as a specialist predator in this multi-prey system may provide insights into the stochastic nature of puma predation on mountain goats. Perhaps the death of one or two specialist pumas may explain the increases in mountain goat survival and future studies could benefit from examining these research hypotheses.

**ACKNOWLEDGEMENTS**

Field support was provided by T. Haffley, K. Cudmore, J. Broecher, T. Benzon, J. Kanta, and L. Meduna.

**ADDITIONAL INFORMATION AND DECLARATIONS**

**Funding**

Funding for this study was provided by South Dakota Department of Game, Fish and Parks. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.
Grant Disclosures
The following grant information was disclosed by the authors:
South Dakota Department of Game, Fish and Parks.

Competing Interests
The authors declare there are no competing interests.

Author Contributions
• Chadwick P. Lehman conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
• Eric M. Rominger analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
• Brady Y. Neiles performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics
The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):
All handling, marking, and monitoring procedures were approved by the South Dakota Department of Game, Fish, and Parks (Permit Numbers 1-3).

Data Availability
The following information was supplied regarding data availability:
Raw data is available as a Supplemental File.
Raw data also includes Program Mark results. Please contact the US Forest Service at: https://www.fs.usda.gov/about-agency/contact-us.
Updated Geospatial Data can be accessed at: https://www.fs.usda.gov/main/blackhills/landmanagement/gis.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.9143#supplemental-information.

REFERENCES
Adams LG, Bailey JA. 1982. Population dynamics of mountain goats in the Sawatch Range, Colorado. Journal of Wildlife Management 46:1003–1009 DOI 10.2307/3808233.
Backsen JC, Howell B. 2013. Comparing aerial detection and photo interpretation for conducting forest health surveys. Western Journal of Applied Forestry 28:3–8 DOI 10.5849/wjaf.12-010.
Bailey JA. 1991. Reproductive success in female mountain goats. Canadian Journal of Zoology 69:2956–2961 DOI 10.1139/z91-416.
Battaglia MA, Smith FW, Shepperd WD. 2008. Can prescribed fire be used to maintain fuel treatment effectiveness over time in Black Hills ponderosa pine forests? Forest Ecology and Management 256:2029–2038 DOI 10.1016/j.foreco.2008.07.026.

Berger J, Wehausen JD. 1991. Consequences of a mammalian predator–prey disequilibrium in the Great Basin Desert. Conservation Biology 5:244–248 DOI 10.1111/j.1523-1739.1991.tb00129.x.

Bergerud AT, Ballard WB. 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. Journal of Wildlife Management 52:344–357 DOI 10.2307/3801247.

Boutin S. 1992. Predation and moose population dynamics: critique. Journal of Wildlife Management 56:116–127 DOI 10.2307/3808799.

Boyce MS, Byrne RL. 2009. Managing predator–prey systems: an update. Transactions of the 74th North American Wildlife and Natural Resources Conference 74:122–124.

Boyd DK, Neale GK. 1992. An adult cougar (Felis concolor) killed by gray wolves (Canis lupus) in Glacier National Park, Montana. Canadian Field Naturalist 106:524–525.

Brandborg SM. 1955. Life history and management of the mountain goat in Idaho. Idaho Wildlife Bulletin 2:1–142.

Broecher J. 2013. Population surveys, survival, and reproduction of resident and translocated (2006/2007) mountain goats in the Black Hills of South Dakota. South Dakota Department of Game, Fish, and Parks Completion Report Number 2013-17. Pierre, South Dakota, USA.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. New York: Springer-Verlag.

Cadsand B, Jex B, Gillingham MP. 2010. Modified clover trap for capturing mountain goats in Northwest British Columbia. Biennial Symposium of the Northern Wild Sheep and Goat Council 17:71–77.

Clover MR. 1956. Single-gate deer trap. California Fish and Game 42:199–210.

Compton BB, Zager P, Servheen G. 1995. Survival and mortality of translocated woodland caribou. Wildlife Society Bulletin 23:490–496.

Cooch EG, White GC. 2009. Program MARK: a gentle introduction. Eighth edition. Available at http://www.phidot.org/software/mark/docs/book/ (accessed on 1 July 2017).

Côté SD, Beaudoin C. 1997. Grizzly bear (Ursus arctos) attacks and nanny–kid separation on mountain goats (Oreamnos americanus). Mammalia 61:614–617.

Côté SD, Festa-Bianchet M. 2001. Reproductive success in female mountain goats: the influence of maternal age and social rank. Animal Behaviour 62:173–181 DOI 10.1006/anbe.2001.1719.

Côté SD, Festa-Bianchet M. 2003. Mountain goat (Oreamnos americanus). In: Feldhamer GA, Thompson BC, Chapman JA, eds. Wild mammals of North America: Biology, management, and conservation. 2nd edition. Baltimore: The Johns Hopkins University Press, 1061–1075.
DeCesare NJ, Hebblewhite M, Robinson HS, Musiani M. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Dwernychuk LW, Boag DA. 1972. Ducks nesting in association with gulls: an ecological trap? Canadian Journal of Zoology 50:559–563 DOI 10.1139/z72-076.

Elbroch LM, Lendrum PE, Allen ML, Wittmer HU. 2015. Nowhere to hide: pumas, black bears, and competition refuges. Behavioral Ecology 26:247–254 DOI 10.1093/beheco/aru189.

Festa-Bianchet M. 1991. The social system of bighorn sheep—grouping patterns, kinship and female dominance rank. Animal Behavior 42:71–82 DOI 10.1016/S0003-3472(05)80607-4.

Festa-Bianchet M, Côté SD. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Washington, D.C.: Island Press.

Festa-Bianchet M, Coulson T, Gaillard JM, Hogg JT, Pelletier F. 2006. Stochastic predation and population persistence in bighorn sheep. Proceedings of the Royal Society B-Biological Sciences 273:1537–1543 DOI 10.1098/rspb.2006.3467.

Festa-Bianchet M, Urquhart M, Smith KG. 1994. Mountain goat recruitment: kid production and survival to breeding age. Canadian Journal of Zoology 72:22–27 DOI 10.1139/z94-004.

Flint RF. 1955. Pleistocene geology of eastern South Dakota. Geological Survey Professional Paper 262. Washington, D.C.: U.S. Government Printing Office.

Goldstein EJ, Rominger EM. 2012. A comparison of mortality rates for desert and Rocky Mountain bighorn sheep under two cougar control regimes. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 18:137–145.

Graham RT, Asherin LA, Battaglia MA, Jain TB, Mata SA. 2016. Mountain pine beetles: a century of knowledge, control attempts, and impacts central to the Black Hills. Gen. Tech. Rep. RMRS-GTR-353. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 193 p.

Hamel S, Côté SD, Smith KG, Festa-Bianchet M. 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. Journal of Wildlife Management 70:1044–1053 DOI 10.2193/0022-541X(2006)70[1044:PDAHPO]2.0.CO;2.

Heisey DM, Patterson BR. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555 DOI 10.2193/0022-541X(2006)70[1544:AROMTE]2.0.CO;2.

Holt RD. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229 DOI 10.1016/0040-5809(77)90042-9.

Horne JS, Garton EO, Krone SM, Lewis JS. 2007. Analyzing animal movements using Brownian Bridges. Ecology 88:2354–2363 DOI 10.1890/06-0957.1.

Hurley MA, Unsworth JM, Zager P, Hebblewhite M, Garton EO, Montgomery DM, Skalski JR, Maylock CL. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33 DOI 10.1002/wmon.4.
Hutchinson GE. 1957. Concluding remarks. population studies: animal ecology and demography. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427 DOI 10.1101/SQB.1957.022.01.039.

Kinley TA, Apps CD. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin* 29:158–164.

Koehler GM, Hornocker MG. 1991. Seasonal resource use among mountain lions, bobcats and coyotes. *Journal of Mammalogy* 72:391–396 DOI 10.2307/1382112.

Kortello AD, Hurd TE, Murray DL. 2007. Interactions between cougars and gray wolves in Banff National Park. *Ecscience* 14:214–222 DOI 10.2980/1195-6860(2007)14[214:IBCPCA]2.0.CO;2.

Laake JL. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013-01. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service. Seattle, Washington.

Larson GE, Johnson RR. 1999. Plants of the Black Hills and Bear Lodge Mountains, South Dakota Agricultural Experiment Station B732. South Dakota State University, Brookings, USA.

Laundre JW, Hernandez L. 2003. Winter hunting habitat of pumas Puma concolor in northwestern Utah and southern Idaho, USA. *Wildlife Biology* 9:123–129 DOI 10.2981/wlb.2003.034.

Lehman CP, Rota CT, Rumble MA, Millsbaugh JJ. 2017b. Characteristics of successful puma kill sites of elk in the Black Hills, South Dakota. *Wildlife Biology* 23:1–10 DOI 10.2981/wlb.00248.

Lehman CP, Rota JD, Raithel CT, Millsbaugh JJ. 2017a. Pumas affect elk dynamics in absence of other large carnivores. *Journal of Wildlife Management* 82:344–353.

Logan KA, Irwin LL. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildlife Society Bulletin* 13:257–262.

Logan KA, Sweanor LL. 2001. *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Washington, D.C.: Island Press.

Mattson DJ, Merrill T. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conservation Biology* 16:1123–1136 DOI 10.1046/j.1523-1739.2002.00414.x.

McCullagh P, Nelder JA. 1989. *Generalized linear models*. Second edition. New York: Chapman and Hall.

Morris WF, Doak DF. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sunderland: Sinauer.

National Climatic Data Center. 2015. *Local climatological data—daily and monthly precipitation data*. Available at [http://cdo.ncdc.noaa.gov](http://cdo.ncdc.noaa.gov) (accessed on 1 July 2016).

Nielson RM, Sawyer H, McDonald TL. 2014. Package BBMM: Brownian bridge movement model. Available at [https://cran.r-project.org/web/packages/BBMM/BBMM.pdf](https://cran.r-project.org/web/packages/BBMM/BBMM.pdf) (accessed on 15 July 2014).

Novaro AJ, Walker RS. 2005. Human-induced changes in the effect of top carnivores on biodiversity in the Patagonian Steppe. In: Ray JC, Redford KH, Steneck RS, Berger
J, eds. *Large carnivores and the conservation of biodiversity*. Washington, D.C.: Island Press, 268–288.

O’Gara BW. 1978. Differential characteristics of predator kills. *Proceedings of the Biennial Pronghorn Antelope Workshop* 8:380–393.

Oli MK. 2003. Partial life-cycle models: how good are they? *Ecological Modelling* 169:313–325 DOI 10.1016/S0304-3800(03)00277-1.

R Development Core Team. 2019. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/.

Rearden SN, Anthony RG, Johnson BK. 2011. Birth-site selection and predation risk of Rocky Mountain elk. *Journal of Mammalogy* 92:1118–1126 DOI 10.1644/09-MAMM-A-019A.1.

Redden JA, Norton JJ, McLaughlin RJ. 1982. Geology of the Harney Peak granite, Black Hills, South Dakota. United States Geological Survey Report Number, 82–481.

Reiter DK, Brunson MW, Schmidt RH. 1999. Public attitudes toward wildlife damage management and policy. *Wildlife Society Bulletin* 27:746–58.

Ripple WJ, Wirsing CC, Wilmers AJ, Letnic M. 2013. Widespread mesopredator effects after wolf extirpation. *Biological Conservation* 16:70–80.

Robinson HS, Wielgus RB, Gwilliam JC. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. *Canadian Journal of Zoology* 80:556–568 DOI 10.1139/z02-025.

Rominger EM. 2018. The Gordian Knot of mountain lion predation and bighorn sheep. *Journal of Wildlife Management* 82:19–31 DOI 10.1002/jwmg.21396.

Rominger EM, Weisenberger ME. 2000. Biological extinction and a test of the conspicuous individual hypothesis in the San Andres Mountains, New Mexico. *Transactions of the North American Wild Sheep Conference* 2:293–307.

Rominger EM, Whitlaw HA, Weybright D, Dunn WC, Ballard W. 2004. The influence of mountain lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993–999 DOI 10.2193/0022-541X(2004)068[0993:TIOMLP]2.0.CO;2.

Rotella JJ, Dinsmore SJ, Shaffer TL. 2004. Modeling nest–survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187–205.

Ruth TK, Haroldson KM, Murphy PC, Buotte MG, Hornocker MA, Quigley HB. 2011. Cougar survival and source–sink structure in the Greater Yellowstone’s northern range. *Journal of Wildlife Management* 75:1381–1398 DOI 10.1002/jwmg.190.

Sargeant GA. 2020. mort: R tools for wildlife research and management. R Package Version 20.01.21. Jamestown, North Dakota, USA: U.S. Geological Survey Northern Prairie Wildlife Research Center. Available at http://cran.r-project.org/web/packages/mort/index.html.

Schmitz OJ, Grabowski BL, Peckarsky EL, Preisser GC, Trussell JH, Vonesh JR. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. *Ecology* 89:2436–2445 DOI 10.1890/07-1030.1.
Serrouya R, McLellan BN, Van Oort H, Mowat G, Boutin S. 2017. Experimental moose reduction lowers wolf density and stops decline of endangered caribou. PeerJ 5:e3736 DOI 10.7717/peerj.3736.

Shepperd WD, Battaglia MA. 2002. Ecology, silviculture, and management of ponderosa pine in the Black Hills. United States Forest Service General Technical Report RMRS–GTR–97. Fort Collins, Colorado, USA.

Smith BL. 1976. Ecology of the Rocky Mountain goat in the Bitterroot Mountains, Montana. M.S. Thesis, University of Montana, Missoula, USA.

Smith BL. 1986a. Longevity of American mountain goats. Biennial Symposium of the Northern Wild Sheep and Goat Council 5:341–346.

Smith CA. 1986b. Rates and causes of mortality in mountain goats in southeast Alaska. Journal of Wildlife Management 50:743–746 DOI 10.2307/3800994.

Smith JB. 2014. Determining impacts of mountain lions on bighorn sheep and other prey sources in the Black Hills. M. S. Thesis, South Dakota State University, Brookings, South Dakota, USA.

South Dakota Department of Game, Fish and Parks. 2017. South Dakota White-tailed Deer and Mule Deer Management Plan, 2017-2023. Completion Report 2017–02. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota, USA.

South Dakota Department of Game, Fish and Parks. 2018. South Dakota Mountain Goat Management Plan, 2018–2027. Completion Report 2018 01. South Dakota Department of Game, Fish and Parks, Pierre, South Dakota, USA.

South Dakota Department of Game, Fish and Parks. 2019. South Dakota Mountain Lion Management Plan: 2019–2029. South Dakota Department of Game, Fish and Parks, Version 2019-06, Pierre, South Dakota, USA.

Stevens V, Houston DB. 1989. Reliability of age determination of mountain goats. Wildlife Society Bulletin 17:72–74.

Swenson JE. 1985. Compensatory reproduction in an introduced mountain goat population in the Absaroka Mountains, Montana. Journal of Wildlife Management 49:837–843 DOI 10.2307/3801355.

Vazquez-Dominguez E, Ceballos G, Cruzado J. 2004. Extirpation of an insular subspecies by a single introduced cat: the case of the endemic deer mouse Peromyscus guardia on Estanque Island, Mexico. Oryx 38:347–350.

Wehausen JD. 1996. Effect of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471–479.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138 DOI 10.1080/00063659909477239.

White KS, Pendleton GW, Crowley D, Griese HJ, Hundertmark KJ, McDonough T, Nichols L, Robus M, Smith CA, Schoen JW. 2011. Mountain goat survival in coastal Alaska: effects of age, sex, and climate. Journal of Wildlife Management 75:1731–1744 DOI 10.1002/jwmg.238.