



Cascading effects of habitat on maternal condition and life-history characteristics of neonatal mule deer

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The condition of maternal female mammals greatly influences life-history characteristics of their young, but interactions between habitat and maternal condition and their combined influences on birth characteristics and survival of neonates are less well understood, especially in free-ranging populations. We monitored survival of neonatal mule deer (*Odocoileus hemionus*) inhabiting 2 contrasting ecotypes in Idaho: aspen woodlands (*Populus tremuloides*) in southeast Idaho (Caribou Mountains) and mixed-conifer grasslands (lodge-pole pine, *Pinus contorta*; Douglas-fir, *Pseudotsuga menziesii*) in central Idaho (Salmon River Mountains). We expected the Caribou Mountains to offer better forage and greater concealment cover than the Salmon River Mountains. We tested for an array of maternal influences on neonatal deer inhabiting those dissimilar ecosystems. We monitored 96 neonates from date of capture to 5 months of age ($n = 44$ in the Caribou Mountains, 2010; $n = 52$ in the Salmon River Mountains, 2011). Survival and birth characteristics consistently diverged between study areas, whereas timing of births was similar. Female deer from the Salmon River Mountains exhibited poor maternal condition and small litter sizes compared with females from the Caribou Mountains. Young from the Salmon River Mountains exhibited lower rates of growth, occupied bedding sites with less concealment cover, and subsequently experienced lower survival from birth to 5 months of age, compared with neonates from the Caribou Mountains. Cause of deaths for young mule deer on both study sites was mostly from predation. Our findings emphasize the potential role that habitat plays in the population dynamics of mule deer via cascading effects on physical condition, reproduction, and survival. Changes in habitat, potentially associated with changing climate, fire regimes, and land uses, probably have contributed to the widespread declines in populations of mule deer during recent decades.

Key words: birth weight, concealment cover, Idaho, *Odocoileus hemionus*, parturition, survival, timing of births

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Mule deer (*Odocoileus hemionus*) have been declining for several decades in the Intermountain West (Bishop et al. 2008; Hurley et al. 2011; Lendrum et al. 2012, 2013). Declines in population size likely have resulted from suppressed recruitment of young rather than reduced survivorship of adults (Eberhardt 1985; Gaillard et al. 2000; Raithel et al. 2007; Monteith et al. 2014) because adult survival is typically high and often stable in ungulates (Gaillard et al. 2000). Accordingly, factors that determine survival of young may dictate population trajectories. Density-dependent mechanisms influence physical condition of ungulates and have consequences for many life-history patterns exhibited by those large mammals, including survivorship

of young (Eberhardt 1985; Gaillard et al. 2000; Kie et al. 2003; Pierce et al. 2012). Previous studies on survival of mule deer documented proximate causes of mortality and population trends for females and their young (Linnell et al. 1995; Bowyer et al. 1998a; Bleich et al. 2006; Lomas and Bender 2007); however, potential links between habitat and nutritional condition of adult females, characteristics of neonates, and subsequent growth and survival of young are less well established for free-ranging populations of mule deer (Tollefson et al. 2010, 2011; Pierce et al. 2012; Monteith et al. 2014).

Nutrition garnered during winter and summer influences most aspects of ungulate biology (Kie et al. 2003; Barboza et al.

2009; Monteith et al. 2013; Simard et al. 2014). Julander et al. (1961) argued persuasively that quality and quantity of forage during summer were the best predictors of herd productivity in mule deer, including rates of ovulation by adult females and birth weights of neonates. Higher-forage quality in summer has positive direct and indirect effects on herd productivity for cervids inhabiting strongly seasonal environments (Bårdsen and Tverra 2012; Tverra and Bårdsen 2013; Monteith et al. 2014). Maternal condition resulting from increased available nutrition affects multiple characteristics associated with reproductive success, including offspring size and rate of growth, timing of births, and litter size (Keech et al. 2000; Bårdsen et al. 2008; Monteith et al. 2009; Freeman et al. 2013). Understanding fitness consequences of maternal condition is contingent upon identifying those traits related to maternal influences, which subsequently influence survival of offspring (Benton et al. 2001; Stewart et al. 2005; Monteith et al. 2009).

Young ungulates face greatest risk of predation in the early stages of life (Bowyer et al. 1998a, 1998b). Although proximate causes of mortality (e.g., predation, drowning, or malnutrition) vary, poor physical condition of females may predispose neonates to early mortality, and characteristics of habitat may interact and contribute to their vulnerability (Monteith et al. 2014). Female cervids in poor physical condition tend to give birth to young with lower birth weights that often suffer high rates of mortality (Clutton-Brock et al. 1987; Keech et al. 2000). Low birth weights of neonates are associated with early mortality in white-tailed deer (*Odocoileus virginianus*—Langenaue and Lerg 1976; Sams et al. 1996; Ditchkoff et al. 2001; Carstensen et al. 2009), moose (*Alces alces*—Keech et al. 2000), reindeer (*Rangifer tarandus*—Bårdsen et al. 2014), and mule deer (Lomas and Bender 2007; Bishop et al. 2009; Monteith et al. 2014). Characteristics of habitat, mainly those that relate to concealment cover, further contribute to the probability of detection by predators and escape once detected (Bowyer 1986; Bowyer et al. 2001; Grovenburg et al. 2012). Consequently, interactions between habitat and physical condition of mothers may determine survival of young (Gaillard et al. 2000; Monteith et al. 2009; Grovenburg et al. 2012; Monteith et al. 2014).

We examined links between body condition of female mule deer and characteristics related to parturition and survival of neonatal mule deer in 2 contrasting ecotypes in Idaho. In Idaho, aspen (*Populus tremuloides*) woodlands provide some of the best forage for mule deer during summer (Beck and Peek 2005), and concomitantly those woodlands may offer concealment from predators (sensu Pierce et al. 2004). Our study areas included a productive summer range dominated by aspen woodlands (Caribou Mountains) and a lower-quality summer range dominated by mixed-conifer grasslands (Salmon River Mountains—Thiel 2012). We compared maternal condition, birth characteristics, and survival of neonates between those 2 ecotypes. We hypothesized that differences in characteristics of maternal females and neonates at parturition would be apparent at the population level (i.e., characteristics of deer would differ between the contrasting ecotypes). We predicted that if

habitat quality was lower in the Salmon River Mountains, there would be lower body condition of maternal females, decreased litter size, later and less synchronous births, neonates exhibiting lower birth weights and slower rates of growth, and poorer survival of neonates than for deer inhabiting the Caribou Mountains. Within each population, we hypothesized that maternal condition would be the best predictor of birth weight and that birth weight would be the main factor (related to nutrition) in determining survival of young. Also, we predicted that greater concealment cover offered by aspen woodlands in the Caribou Mountains would result in higher survivorship of young than in the Salmon River Mountains.

MATERIALS AND METHODS

Study areas.—We examined life-history characteristics and survival of neonatal mule deer in each of 2 diverse areas: Caribou Mountains in southeast Idaho (43°45'N, 111°14'W) and Salmon River Mountains in central Idaho (44°27'N, 114°30'W). Mule deer were migratory, concentrating on lower elevation winter range and moving to higher elevation summer range within each study area, a pattern typical of mule deer in Idaho (Stewart et al. 2009). Elevations and temperatures were similar between areas; however, precipitation and snowfall were greater during summer and winter in Caribou Mountains compared with Salmon River Mountains (Western Regional Climate Center, 1983–2013; Table 1). Weather stations were located within 48 km of the corresponding study areas. Although the magnitude of average precipitation and temperature varied between study areas, the general pattern of precipitation ($r = 0.53$, $P < 0.05$) and temperature ($r = 0.98$, $P < 0.001$) was similar between study sites across months. The winter before capture of neonates in the Caribou Mountains (2010–2011) was mild compared with average snowfall on that winter range (62% of average), whereas deer from the Salmon River Mountains experienced greater snowfall (130% of average) on winter range during the winter before capture than the long-term average (Western Regional Climate Center, 1983–2013; Table 1).

Study areas in southeast and central Idaho represented substantially different ecotypes, both of which were essential summer ranges for mule deer. Vegetation composition of the Caribou Mountains was dominated by aspen, maple (*Acer glabrum*), and Douglas-fir (*Pseudotsuga menziesii*). The Salmon River Mountains were characterized by mixed-conifer grasslands and consisted of fewer herbaceous plants compared with the Caribou Mountains (Thiel 2012). Aspen woodlands supported greater diversity of plants (Kuhn et al. 2011), whereas coniferous forests had decreased shrub-understory production and diversity (Kranz and Linder 1973; Bartos and Mueggler 1982). Based on diet composition and selection, forage abundance and quality (crude protein and in vitro dry matter digestibility), and fecal nitrogen (Leslie et al. 2008), habitat quality for mule deer was substantially better in the Caribou Mountains than in the Salmon River Mountains (Thiel 2012). Densities of mule deer wintering in the Caribou Mountains were higher

Table 1.—Comparison of environmental factors for 2 migratory populations of mule deer (*Odocoileus hemionus*) inhabiting the Caribou Mountains and Salmon River Mountains, Idaho, on a) summer and b) winter ranges. Study year includes the gestation of young through monitoring of their survival.

	Caribou Mountains		Salmon River Mountains	
	30-Year average	Study year	30-Year average	Study year
a) Summer range				
Temperature summer, °C (range)	4.1–28.0	4.9–25.8	2.4–26.6	1.2–27.2
Total precipitation, cm (\pm SD)	45.3 (7.0)	42.5	23.5 (16.3)	49.2
Total snowfall, cm (\pm SD)	264.7 (127.8)	273.1	174.3 (61.0)	229.4
Elevation, m (range)	1,815–2,225		1,880–2,195	
b) Winter range				
Temperature winter, °C (range)	–12.7–0.9	–14.3–2.9	–14.1–2.4	–14.0–2.7
Total precipitation, cm (\pm SD)	36.1 (9.8)	31.3	30.5 (7.1)	30.5
Total snowfall, cm (\pm SD)	136.3 (61.9)	84.8	70.5 (38.2)	92.3
Elevation, m (range)	1,560–1,945		1,590–2,130	

(25.8 deer/km²) than those in the Salmon River Mountains (1.6 deer/km²—J. Rachael, in litt., Idaho Department of Fish and Game), but data were not available for summer. Such differences in winter densities of deer can be misleading because varying winter conditions, especially snow depth, can concentrate deer (Atwood 2009), and relative quality and quantity of forage may support different abundances of deer (Pierce et al. 2004; Monteith et al. 2014). Moreover, values from winter may not be representative of summer range for migratory deer, where density in relation to plant production likely plays a critical role in determining productivity of mule deer (Julander et al. 1961). Predators of young deer on both study areas included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*); data on density of predators were not available.

Scoring body condition of maternal deer.—We obtained an ocular score of body condition of what appeared to be mostly adult (≥ 2 year) females using a modified version of the Riney method, which was based on the visible prominence of skeletal points on hips, pelvic girdle, sacral and lumbar ridges, and ribs (Riney 1960; Atwood 2009). This assessment relies on body mass (muscle and fat) associated with a number of visible bone structures in ungulates. A score of 5 corresponded to no bone points being visible on an animal (unable to see depressions or outline of the ribs, lumbar, and sacral ridge is rounded and smooth; tail bone is rounded; and hip bones are smooth—excellent condition), score of 3–4 corresponded with 1–2 points visible (depression or prominent protrusion of the hip or sacral ridge present—good condition), score of 2 was determined by having 3 visible points (depression or prominent protrusion of the hip, sacral ridge appears as a knife-like blade, and lumbar ridge is visible—fair condition), and a score of 1 represented 5 visible points (all points plus outline of ribs is clear—poor condition). Riney (1982) noted that although such ocular estimates entailed some subjectivity, those metrics were useful in documenting condition of deer occupying different habitats.

We evaluated body condition using spotting scopes (10 \times 60 magnification), with 3 trained individuals, who made consistent observations on condition of deer at a distance of ≤ 200 m. Observers trained together until their scores were consistent

with one another. The same 3 observers scored deer in both study years. An average score was used when occasional disagreements occurred between observers. The 1st author (JRST) was involved in scoring all deer; 2 of 3 individuals scored 90% of deer, and remaining deer were scored only by JRST. We ensured the mother of a particular neonate was identified by observing nursing or other maternal behavior between the radiocollared neonate and female at time of data collection.

Data collection for neonates.—We captured neonatal mule deer during 1–18 June, which encompassed peak parturition (Long et al. 2009; Hurley et al. 2011). We captured 44 neonates in the Caribou Mountains in 2010 and 52 neonates in the Salmon River Mountains in 2011. We captured neonates by hand, aided by crews using spotting scopes (60 \times magnification) to monitor behaviors of maternal deer that would indicate the presence and location of neonates (White et al. 1972; Riley and Dood 1984; Bowyer et al. 1998a; Hurley et al. 2011). We attempted to capture all neonates belonging to each maternal female, and we monitored females for sufficient duration to document all young. In a few instances, however, we were only able to capture 1 of the neonates because a twin already had fled. We collected both morphological and behavioral characteristics of neonates at time of capture. We characterized behavioral data into the ability to run (unable to stand, ≤ 1 day old; somewhat wobbly, 1–3 days old; or very sturdy, ≥ 2 days old) and degree of stress (calm, 1–4 days old; vocalizing, ≥ 2 days old; or struggling, ≥ 3 days old) to facilitate estimating age at capture. We obtained morphological measurements of new hoof growth (mm), chest girth (cm), hind-foot length (cm), capture weight (kg), softness of hoof surface, wetness of hair, and condition of the umbilicus (Robinette et al. 1973). We recorded measurements with digital scales (0.01 kg), calipers (0.1 mm), and flexible cloth tapes (0.5 cm). We determined date of birth for each neonate by the appearance of hooves, length of new hoof growth, condition of the umbilicus, and behavior (Robinette et al. 1973; Brinkman et al. 2004; Pojar and Bowden 2004; Grovenburg et al. 2014a). Measurement of new hoof growth was used to calculate age of neonates ≥ 1 day of age (Robinette et al. 1973; Brinkman et al. 2004). Estimated age at capture of neonates, combined with weight at capture, allowed us to back-calculate weight at birth

for each neonate based on the slope of a least-squares regression line developed for each study area. We assumed weight at capture for neonates ≤ 24 h old represented weight at birth (Robinette et al. 1973). We knowingly traded potential temporal variation in study areas between years to acquire adequate sample sizes for each area within a year.

We monitored neonatal survival with expandable, mortality-mode VHF radiocollars that had a battery life of ≥ 1 year (Advanced Telemetry Systems, Isanti, Minnesota). We monitored neonates every 2 days using ground-based telemetry for their first 3 months and every 2 weeks by ground or aerial telemetry (Cessna 180) from 1 September through 30 November in 2010 (Caribou Mountains) and 2011 (Salmon River Mountains). All mortalities were investigated within 48 h of being detected to determine cause-specific mortality and to recover radiocollars. When whole carcasses were recovered, we sent them to the Idaho Department of Fish and Game Wildlife Health Laboratory in Nampa, Idaho, to determine cause of death. Young that showed signs of mortality caused indirectly by capture were censored from survival analyses ($n = 2$). In addition, neonates that shed their collars were censored from further analyses because we assumed their fate was independent of collar failure (Caribou Mountains, $n = 1$; Salmon River Mountains, $n = 6$ —Grovenburg et al. 2014b). Methods of capturing and studying neonates were approved by an independent Institutional Animal Care and Use Committee at Idaho State University (Protocol #6770510) and were consistent with the American Society of Mammalogists guidelines for research on wild mammals (Sikes et al. 2011).

We determined percent concealment cover at bed sites of neonates using a 2-m tall cover pole (Griffith and Youtie 1988; Bowyer et al. 1998b). We observed the cover pole from 10 m at a standing height (1.5–1.8 m) from each of 4 directions (up-slope, 2 cross-slopes, and down-slope) and recorded the proportion of 0.5-m segments that were $\geq 50\%$ obscured from view (Bowyer et al. 1998b). Subsequently, we averaged the proportion of concealment cover across the 4 directions to provide an overall estimate of concealment cover for a particular location. Measurements of cover during summer were associated with the time of greatest predation risk to neonates because this risk was highest during the first 2 months following parturition (Bowyer et al. 1998b; Ballard et al. 2001; Pojar and Bowden 2004; Hurley et al. 2011). Generally, twins were bedded together (≤ 5 m apart); in instances that twins of the same litter were not captured together, the measurement from the captured neonate was used for the litter mate to characterize concealment. A 2nd measurement of concealment cover at bed sites was determined for neonates 4–6 weeks old, which represented use of cover at peak lactation for maternal females (Sadleir 1982).

Statistical analyses.—We analyzed characteristics related to parturition and maternal condition at 3 levels: the population level, the maternal level, and the level of the individual neonate. At the population level, we used multiple regression to determine growth rate (kg/day) of neonates and effect of study area (PROC GLM—Littell et al. 2006). Neonatal growth rate

was determined by regressing estimated ages at capture against weights at capture. Following a significant ($P < 0.05$) main effect of study area, we determined the slope of the best-fitting line for growth rate for each area from least-squares regression (PROC GLM, SAS). We visually inspected residuals to determine if assumptions of equal variance, normality, and linearity for both areas were met. Growth rate was then used to back-calculate weight at birth, based on the slope of the line for those neonates > 1 day of age in each study area.

Animals born with different weights may show dissimilar absolute rates of growth over time; thus, a measure of relative growth is needed to account for initial differences in size (Hunt 1982). Consequently, we estimated a mean rate of relative growth for each study area (Hunt 1982):

$$\bar{R}_{1-2} = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1}, \quad (1)$$

where W_1 is weight at time T_1 , and W_2 is weight at time T_2 . We used predicted growth rates derived from the regression equation of weights relative to age for each area because individual animals could not be weighed repeatedly. Mean relative growth rate, \bar{R}_{1-2} , is an increase in neonate weight per unit of neonate weight per unit time (i.e., initial differences in weight are factored out). We determined if a difference in relative mean rate of growth by study area existed by visually inspecting the derived growth lines (i.e., lines of growth rates without overlap indicated difference in rate with regard to study area).

We used multivariate analysis of covariance (MANCOVA) to determine if characteristics of maternal females during parturition (i.e., maternal condition, timing of births, total litter weight, and concealment cover at 0–50, 50–100, and 100–200 cm in height) differed between study areas (i.e., fixed effect), while accounting for effects of litter size as a covariate. We conducted 2 separate MANCOVAs, 1 for each time frame (parturition and peak lactation). Following a significant main effect of study area, we used canonical correlation analysis to evaluate variables that contributed most to those differences, which we then analyzed separately in 1-way analyses of covariance (ANCOVAs) to test for differences with respect to study area (Zar 1999); we acknowledge, however, that those ANCOVAs were not completely statistically independent. Births of unknown litter size were excluded from this test ($n = 2$ in Caribou Mountains; $n = 3$ in Salmon River Mountains), as were instances when only 1 twin was captured and, thus, total weight of the litter could not be determined ($n = 4$ in Caribou Mountains; $n = 1$ in Salmon River Mountains). For concealment cover, we averaged cover measurements for individuals of the same litter because litter was the sampling unit for this analysis. Plots of residuals were inspected visually for agreement with assumptions of ANCOVA. We evaluated timing and synchrony (SD) of births (Rachlow and Bowyer 1991; Whiting et al. 2011, 2012) for population-level differences by observing whether 95% confidence interval (CI) overlapped. We used the 2-sample z -test for proportions to examine differences in

proportions of neonates killed by predators in the 2 study areas (Zar 1999). We adopted an $\alpha = 0.05$ for statistical tests.

We used a linear mixed effects model (PROC MIXED—Littell et al. 2007) to determine variables responsible for estimated birth weight. Predictor variables included body condition of the maternal deer, litter size, timing of birth, and study area. We also considered the interactions study area \times body condition and body condition \times litter size. We used Pearson's correlation coefficient to evaluate collinearity between predictor variables; none of the aforementioned variables had $r \geq |0.50|$ (Neter et al. 1996). We included maternal identity (ID) as a random effect (intercept), which accounted for lack of independence among neonates from the same litter. We used an information theoretic approach for model selection and to evaluate variable importance by calculating Akaike's information criteria corrected for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i) for each survival model (Burnham and Anderson 2002). Before formal model selection, we fit a global model that included all predictor variables and relevant interactions. At this step, we removed variables that were clearly uninformative (i.e., 85% *CI* overlapped 0) from further analyses (Arnold 2010). We then considered all possible combinations of remaining predictor variables that we postulated would affect birth weight of neonatal mule deer (Arnold 2010; Doherty et al. 2010; Monteith et al. 2011). We inspected residual plots for agreement with assumptions of regression. We used AIC_c to determine the most parsimonious model (Burnham and Anderson 2002) and considered all models with $\leq 2 \Delta AIC_c$ units as competing for the best model.

We used known-fate modeling in program MARK (White and Burnham 1999) to estimate survival and determine factors that influenced survival of neonates from birth to 22 weeks. Events, based on encounter histories, were segmented into 1-week intervals because estimates of survival converge using 1-week intervals when birth date is determined based on estimated age at capture (Grovenburg et al. 2014a). Neonates entered the model based on age at capture; neonates ≤ 1 week old at capture entered the survival analysis in the 1st interval, those ≥ 1 week old but ≤ 2 -week olds entered the 2nd interval, and so on. Neonates that shed their collars prematurely, or those not encountered during an interval, were censored from that interval. To identify periods of time when survival remained constant, we plotted survival on a weekly basis by allowing survival to vary randomly by week (Barber-Meyer et al. 2008). Within each study area, survival varied during weeks 1–4 but remained relatively constant from weeks 5 through 22. Therefore, we designed a stage-specific model that permitted survival to vary during weeks 1–4 and survival to remain constant thereafter. We selected this stage-specific model from among others with different temporal constraints using AIC_c ; there were no other candidate models within $\Delta AIC_c < 2$ (Burnham and Anderson 2002).

We retained the stage-specific model of survival and added covariates to evaluate the influence of other characteristics on summer survival of young, including variables associated with habitat and maternal condition. Candidate predictor variables

associated with habitat at the individual level were concealment cover at time of capture and again between 4 and 6 weeks at heights of 50, 100, and 200 cm. Predictor variables for individual neonates related to birth characteristics were age of neonate at capture, weight at birth, Julian date of birth, days from mean date of birth, litter size, and sex. We specifically added age at capture as a predictor variable because neonates are particularly susceptible to mortality during the first few days of life, and this variable helps to control for not capturing more neonates at birth. We also included study area as a predictor variable at the population level because we were interested in determining differences in survival of young between areas. Interactions considered were birth weight \times litter size, birth weight \times maternal condition, and litter size \times maternal condition. We again used an information theoretic approach for model selection and to evaluate variable importance with an identical approach to that used in the analysis of birth weight.

We attempted to radiocollar all neonates from each maternal female; thus, survival for siblings may not have been completely independent because they shared maternal resources and occupied similar habitats (Bishop et al. 2008). We used bootstrap analysis in program MARK by resampling litters of adult females rather than individual young to generate 10,000 replicates—the maternal female was the sample unit ($n = 60$) rather than individual neonates ($n = 94$ —Bishop et al. 2008). We conducted bootstrap analyses based on a fully time-dependent model to avoid misinterpreting overdispersion for lack of model fit (Bishop et al. 2008). We approximated overdispersion by dividing the theoretical variance by the estimate of observed variance established from the bootstrap analysis (Bishop et al. 2008). Our calculated estimate of overdispersion averaged 1.09 (Caribou Mountains = 1.00; Salmon River Mountains = 1.18), which was less than values reported previously for mule deer in Colorado and California (1.25—Bishop et al. 2008; and 1.18—Monteith et al. 2014, respectively). For all subsequent estimates of survival, we used the variance inflation factor ($\hat{c} = 1.09$) to correct for overdispersion.

RESULTS

Maternal condition and birth weights of young.—Initial reduction in variables (based on 85% *CI* overlap of 0) for birth weight of neonates resulted in the removal of all variables and interaction terms except litter size and maternal condition; weights of neonatal mule deer increased with better maternal condition and smaller litter sizes. The best model incorporated maternal condition and litter size, including only each individual term resulted in $\Delta AIC_c > 11$. Models indicated that birth weight of mule deer increased 0.32 kg (95% *CI* = 0.22–0.72 kg) with every 1-unit increase in maternal condition at parturition and that birth weight increased by 0.47 kg (95% *CI* = 0.20–0.44 kg) in singletons compared with twins. The absence of an effect of study area on birth weight indicated that differences in birth weight between the Salmon River and Caribou Mountains probably were explained by the disparity in maternal condition of deer between the 2 regions.

Population-level differences in birth characteristics.—Mule deer from the Caribou Mountains generally exhibited life-history characteristics associated with higher-quality habitat than those inhabiting the Salmon River Mountains (Table 2). Condition of maternal females, litter size, and litter weights were greater in the Caribou Mountains than in the Salmon River Mountains (Table 2). Mean age at capture ($\pm SE$) for neonates from the Caribou Mountains was 2.2 ± 0.30 days, and for neonates from the Salmon River Mountains, it was 4.3 ± 0.42 days. Proportion of neonates that were female and timing and synchrony of births were nearly identical between study areas (Table 2).

When we controlled for litter size as a covariate, other birth and habitat variables differed between maternal deer inhabiting the 2 study areas (Wilk's λ at parturition = 0.62, $F_{6,42} = 4.21$, $P < 0.002$; Wilk's λ at peak lactation = 0.63, $F_{4,21} = 3.14$, $P = 0.036$). Canonical correlation analysis indicated maternal condition, total litter weight, and concealment cover at 0–50 cm in height at parturition, and maternal condition and concealment cover at 0–50 cm in height at peak lactation contributed most to overall significance of results of the MANCOVA. Maternal condition, litter weight of twins, and concealment cover of young were greater for deer inhabiting the Caribou Mountains than for those occurring in the Salmon River Mountains (Table 2). Separate univariate ANCOVAs supported differences in total litter weight at parturition ($F_{2,47} = 63.6$, $P < 0.001$), body condition of maternal deer at parturition ($F_{2,47} = 12.3$, $P < 0.001$) and peak lactation ($F_{2,24} = 3.78$, $P = 0.037$), and concealment cover at a height of 0–50 cm at peak lactation ($F_{2,24} = 5.28$, $P = 0.013$), but not at parturition ($F_{2,47} = 1.29$, $P = 0.28$). Twinning rates were significantly higher for mule deer in the Caribou Mountains than for deer in the Salmon River Mountains ($\chi^2 = 13.04$, $P \leq 0.001$, $n = 57$; Table 2). Furthermore, twins from the Caribou Mountains were significantly heavier than twins from the Salmon River Mountains ($t_{32} = 2.66$, $P = 0.012$; Table 2).

Multiple regression indicated that growth rates, based on the relationship between age and weight at capture, differed between study areas ($P = 0.016$). Separate regressions for each study area indicated that neonatal deer from the Caribou Mountains had a higher growth rate (0.413 ± 0.037 kg/day; $r^2 = 0.75$, $P < 0.001$, $n = 43$) compared with young from the Salmon River Mountains (0.302 ± 0.024 kg/day; $r^2 = 0.76$, $P < 0.001$, $n = 52$; Fig. 1A). Relative growth rate was initially high for neonates in both areas and decreased with time; neonates from the Caribou Mountains maintained a consistently higher growth rate than neonates from the Salmon River Mountains thereafter (Fig. 1B).

Survival of neonates.—Mean ($\pm SE$) survival of young was greater for neonates inhabiting the Caribou Mountains ($\bar{X} = 0.57 \pm 0.076$) than for neonates from the Salmon River Mountains ($\bar{X} = 0.30 \pm 0.063$). The survival model with the lowest AIC_c included study area, concealment cover, and stage-specific survival (Table 3). Survival of neonates varied as a function of study area and concealment cover at 0–50 cm (Table 3), with greater concealment cover at the neonatal bed site having a positive effect on survival of young (Fig. 2). The same model without study area was competitive ($\Delta AIC_c = 1.75$; Table 3). Inclusion of concealment cover with study area reduced the magnitude of the effect of study area and resulted in a parameter estimate that overlapped 0, indicating that differences in survival between study areas were caused largely by the disparity in concealment cover at a height of 0–50 cm (Table 4).

Known causes of death for young mule deer were mostly predation and were slightly but significantly ($Z = 2.97$, $P = 0.003$) higher in the Caribou Mountains (13%) than in the Salmon River Mountains (11%). Of those mortalities caused by predators, most were from unconfirmed predators (50% in Caribou Mountains; 36% in Salmon River Mountains), followed by black bears (20% in Caribou Mountains; 43% in Salmon

Table 2.—Descriptive statistics for neonatal mule deer (*Odocoileus hemionus*) from 2 contrasting study areas in Idaho, 2010 and 2011. The Caribou Mountains contain higher quality habitat than the Salmon River Mountains.

Characteristics	Caribou Mountains			Salmon River Mountains		
	\bar{X}	SE	n	\bar{X}	SE	n
Maternal condition (5 = best, 1 = worst)						
Parturition	3.81	0.12	26	2.74	0.14	34
Peak lactation	3.33	0.18	18	2.47	0.17	17
Litter size (young/female)	1.96	0.04	24	1.52	0.09	33
Julian birth date (days)	157.69	1.04	26	156.67	0.84	36
Birth weights (singletons, kg)	3.59		1	2.92	0.11	16
Birth weights (twins, kg)	2.89	0.08	36	2.48	0.09	22
Sex of neonates (proportion of female)	0.56	0.08	44	0.56	0.07	52
Neonatal concealment cover, 0–50 cm (%)						
Parturition	77.30	3.69	25	69.86	3.82	35
Peak lactation	94.29	2.69	14	80.46	4.77	19
Neonatal concealment cover, 50–100 cm (%)						
Parturition	26.70	4.91	25	19.07	2.93	35
Peak lactation	66.25	6.47	14	48.82	7.42	19
Neonatal concealment cover, 100–200 cm (%)						
Parturition	12.25	3.88	25	7.86	2.19	35
Peak lactation	28.63	7.86	14	30.46	6.62	19

River Mountains), coyotes (30% in Caribou Mountains; 7% in Salmon River Mountains), bobcat (7% in Salmon River Mountains), and golden eagles (*Aquila chrysaetos*; 7% in Salmon River Mountains). Other sources of mortality, with both study areas combined, were low and included aggression from elk and other mule deer (3%), malnutrition (3%), drowning (2%), and vehicle collisions (1%); 2% of mortalities were from unknown causes.

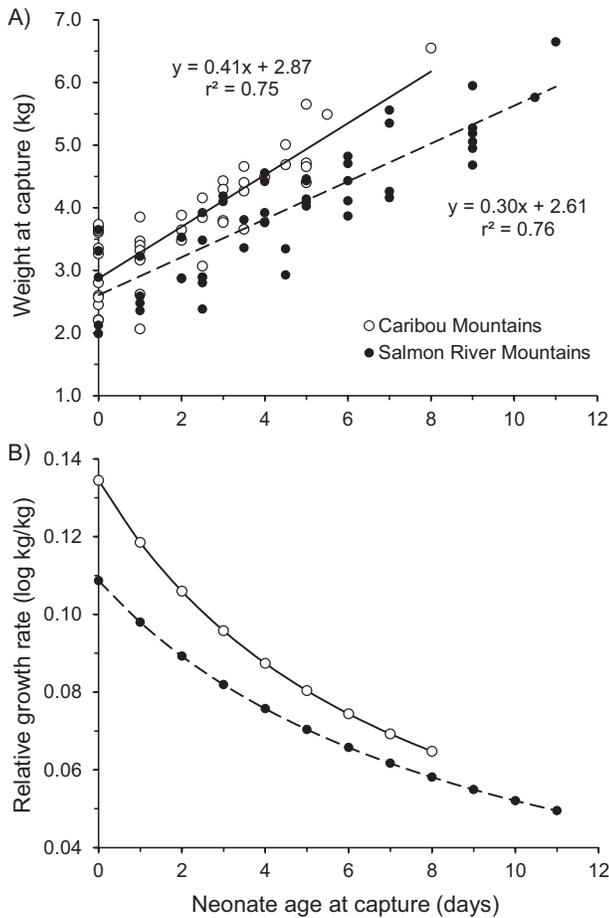


Fig. 1.—A) Difference in absolute growth rates of neonatal mule deer (*Odocoileus hemionus*) based on estimated age of neonates at capture against weights at capture by study area for 2010 and 2011, Idaho. Estimated age was determined from hoof-line growth measurements of each neonate. B) Relative growth rate (kg/kg/day = day⁻¹) factors out the size of animals to establish a difference in growth rate by area using predicted weights by daily intervals from regressions in A.

DISCUSSION

Maternal condition and life-history characteristics of neonates.—Females from the Salmon River Mountains exhibited lower maternal condition, smaller litter sizes, slower growth rate of neonates, lower birth weights, and poorer survival compared with deer residing in the Caribou Mountains. Our findings emphasize the critical role that quality of habitat plays in the population dynamics of mule deer, with cascading effects on physical condition, reproduction, and survival of neonates—all important components of fitness. Contrasting 2 areas with differing quality and quantity of habitats (Thiel 2012) allowed us to observe a more complete range of potential maternal and habitat influences on birth characteristics and subsequent growth and survival of free-ranging mule deer than previously reported. Conducting this landscape-scale study in both areas simultaneously would have been ideal, but fiscal and logistical constraints precluded us from doing so. Nevertheless, the directionally consistent and often stark contrasts in neonatal characteristics and survival support a nutritional underpinning to population dynamics observed in each region.

Female ungulates in poor condition are more likely to have low rates of reproduction and to give birth to small young, which in turn experience high mortality (Kie and White 1985; Bowyer 1991;

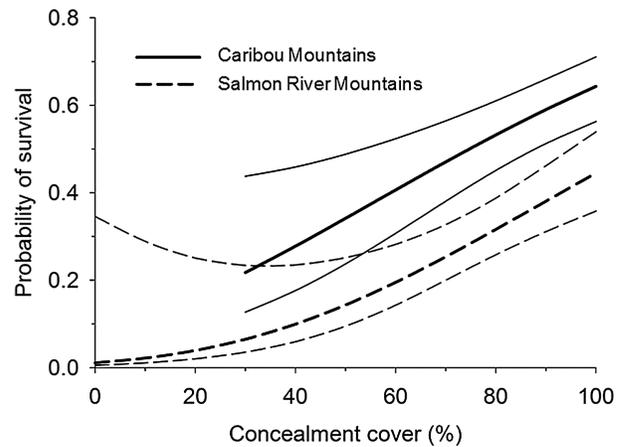


Fig. 2.—Probability of survival (\pm SE) from birth to 5 months for mule deer (*Odocoileus hemionus*) as a function of percent concealment cover at 0–50 cm in height at neonatal bed sites measured at birth and at 4- to 6-week postparturition in the Caribou Mountains ($n = 43$) and the Salmon River Mountains ($n = 51$), Idaho. Predictions are based on the best model that included stage-specific survival, study area, and percent concealment cover.

Table 3.—Ranking of models estimating the survival probability of neonatal mule deer (*Odocoileus hemionus*) from birth to 22 weeks of age in southeastern (Caribou Mountains) and central (Salmon River Mountains) Idaho, 2010 and 2011. The top 2 models were retained as the best models. Stage represents weeks 1–4 with survival allowed to vary, and weeks 5–22 with constant survival, resulting in 5 parameters of time. Concealment is the percentage of cover from a height of 0–50 cm at the neonatal bed site during parturition and again at peak lactation.

Model	AIC _c	Δ AIC _c	AIC _c w _i	Number of parameters	Deviance
Stage + study area + concealment	389.38	0.00	0.57	7	375.29
Stage + concealment	391.12	1.75	0.24	6	379.06
Stage + study area	391.74	2.36	0.18	6	379.67
Stage	396.44	7.06	0.02	5	386.40

Table 4.—Parameter estimates (β) and 95% CI for the top 3 ranking models of survival probability of neonatal mule deer (*Odocoileus hemionus*) from birth to 22 weeks of age in southeastern (Caribou Mountains) and central (Salmon River Mountains) Idaho, 2010 and 2011. Stage represents weeks 1–4 with survival allowed to vary and weeks 5–22 with survival set as a constant. Concealment is the percentage of cover from a height of 0–50 cm at the neonatal bedding site during parturition and again at peak lactation.

Model	Factor	β	95% CI
Stage + study area + concealment	Study area	0.616	–0.174 to 1.250
	50-cm concealment	0.018	0.002 to 0.035
Stage + concealment	50-cm concealment	0.023	0.007 to 0.039
Stage + study area	Study area	0.787	0.176 to 1.398

Bartmann et al. 1992; Sams et al. 1996). Although we observed smaller young born to females in poor condition, we lacked evidence that neonatal mortality was a direct function of birth weight; this outcome may result from the combination of overdispersion, radiocollars shed early in the study, or lack of ability to document all early mortalities. If capture efforts had encompassed the entire distribution of births, including the right-hand tail, then we might have observed stronger links among survival of young, timing of births, maternal condition, and birth weight. Therefore, given a mean age at capture of 4.3 days old in the Salmon River Mountains, we likely missed some early mortality, when effects of birth weight on survival often are manifested (Gilbert et al. 2014; Monteith et al. 2014). For example, early mortality was linked to low birth weight in red deer (*Cervus elaphus*—Albon et al. 1987), moose (Keech et al. 2000), white-tailed deer (Carstensen et al. 2009), and mule deer (Bishop et al. 2009).

Maternal influences on growth of young.—Maternal condition during gestation predicted lifelong consequences of growth in male white-tailed deer (Monteith et al. 2009); young born to females in poor physical condition experienced slow growth despite being offered high-quality foods. The difference in neonatal growth rates between our study areas provides support for their observations because neonates experienced lower rates of growth in the area where maternal deer exhibited poorer body condition. Moreover, relative and absolute growth rate for neonates from the Salmon River Mountains may be overestimated because small young generally experience higher mortality, leaving mostly larger neonates to capture; thus, the divergence in growth rates of young between our study areas likely was underestimated. Ungulates rely on fat stores amassed during summer to survive winter (Unsworth et al. 1999; Cook et al. 2004; Bishop et al. 2005; Taillon et al. 2006); consequently, forage quality and quantity during spring and summer are critical for weight gain and survival of cervids inhabiting temperate environments (Monteith et al. 2013; Morano et al. 2013; Hurley et al. 2014). Body weight of young cervids at the onset of winter is one of the most influential factors on overwinter survival (Keech et al. 2000; Bishop et al. 2005). Differences in forage quality and population density (sensu Kie et al. 2003) between our study areas also may contribute to differences in growth rate and recruitment of young; this potential interaction

between forage quality and population density warrants further study.

Interactions among forage, weather, and life-history characteristics.—For black-tailed deer (*O. hemionus*), recruitment of young was correlated with both deer density and available forage (Gilbert and Raedeke 2004). Deer at or near carrying capacity (K) would be hypothesized to be in poor physical condition because of increased intraspecific competition for limited resources (McCullough 1979; Kie et al. 2003). If we use life-history characteristics related to maternal physical condition to help understand the relationship of the populations to K (sensu Kie et al. 2003; Stewart et al. 2005; Pierce et al. 2012; Monteith et al. 2014), mule deer inhabiting the Salmon River Mountains, which ostensibly are at lower density than in the Caribou Mountains, likely are closer to K because of the poorer physical condition of females and lower survivorship of young, although we caution that we lack data on densities of deer during summer. Habitat in the Caribou Mountains is composed of numerous aspen patches with a greater abundance of forbs compared with the mixed-conifer grasslands of the Salmon River Mountains (Thiel 2012), indicating that habitat differences may influence nutrition and likely affect K (Hobbs and Swift 1985). Weather variables also may interact with population density to exacerbate effects of physical condition on reproduction and survival of young. Individuals in poor physical condition are not well buffered against extreme effects of weather (weather also may adversely influence abundance or availability of forage); indeed, negative effects of weather may be intensified at higher density and lessened at lower density as a result of interactions with density-dependent factors (Milner et al. 1999; Kie et al. 2003; Bårdsen et al. 2011). At sufficiently high density, however, density-dependent mechanisms may override weather-related effects on reproduction (Stewart et al. 2005). Nonetheless, we cannot completely rule out effects of winter weather on reproduction of females and survival of young, especially in the Salmon River Mountains. Forage abundance may mediate effects of density and climate on body mass of deer in autumn (Giroux et al. 2014), and carry-over effects of nutritional reserves may be more common than previously thought (Monteith et al. 2013; Giroux et al. 2014). We believe our results on life-history characteristics of mule deer are sufficient to infer that habitat quality was a major contributor to the patterns we observed. Furthermore, other studies failed to link winter severity with birth characteristics of young in white-tailed deer (Powell and DelGiudice 2005; Carstensen et al. 2009) and caribou (*R. tarandus*—Adams 2005).

Timing of parturition.—Dates of conception and synchrony of births in deer may be related to onset of spring green-up (Parker et al. 2009) and condition of females (McGinnis and Downing 1977; Robinette et al. 1977; McCullough 1979); however, maternal condition did not affect timing of parturition. Our study areas were different with respect to dominant forage species, forage quality (Thiel 2012), and precipitation; therefore, we believe that weather during winter (2010 and 2011) was not a major contributor to timing of parturition because of other natural differences that occurred between areas. That is not

to say, however, that winter ranges were not partially responsible for differences in maternal nutrition and thereby timing of parturition because nutrition carries over between seasons for animals that partially rely on stored capital for reproduction (Monteith et al. 2013, 2014).

Neonatal survivorship and concealment cover.—We hypothesized that survival would be lower in the Salmon River Mountains compared with the Caribou Mountains not only because of better maternal nutrition in the aspen woodlands but also because of greater concealment cover. Although our results did not support a direct effect of maternal nutrition, there were large differences (27%) in survival of neonatal mule deer between areas. Differences in concealment cover accounted for a large portion of the disparity in survival between study areas; concealment cover of neonatal bedding sites was, on average, 15% lower in the Salmon River Mountains compared with the Caribou Mountains and ostensibly was responsible for lower survival of young in the Salmon River Mountains. Characteristics of habitat used by neonatal white-tailed deer in the Great Plains influenced initial detection by a predator, and once a chase ensued, the habitat into which neonates fled affected their probability of being captured (Grovenburg et al. 2012). Although we did not measure density of predators, which also can influence survival of young (Griffin et al. 2011), we postulate that habitat in the Caribou Mountains not only offered greater nutritional resources to female mule deer but also yielded greater protection from predation risk. Indeed, the positive effect of concealment cover was consistent in both areas, but the Caribou Mountains afforded neonates more opportunity for predator evasion via greater concealment cover.

Compared with deer from the Salmon River Mountains, neonatal mule deer from the Caribou Mountains experienced higher survival and had greater cover for concealment, and females exhibited better body condition and obtained diets of higher quality (Thiel 2012). Thus, we suggest that habitats in the Caribou Mountains provided adequate concealment cover for neonates while also providing forage of high quality (sensu Pierce et al. 2004). Better habitat quality in the Caribou Mountains also resulted in higher rates of growth for young deer in the Caribou Mountains compared with the Salmon River Mountains. Our research, in addition to other recent studies (Bishop et al. 2009; Hurley et al. 2011; Monteith et al. 2014), underscores the potential for habitat to affect the population dynamics of mule deer through cascading effects on physical condition and reproduction of adults and survival of young. Changing climate, fire regimes, and land uses (Lenart et al. 2002; Stenseth and Mysterud 2002; Stewart et al. 2002; Maier et al. 2005) probably have contributed to the extensive declines in mule deer during recent decades.

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