



Original Article

Effects of Male-Biased Harvest on Mule Deer: Implications for Rates of Pregnancy, Synchrony, and Timing of Parturition

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ABSTRACT Evaluating how management practices influence the population dynamics of ungulates may enhance future management of these species. For example, in mule deer (*Odocoileus hemionus*), changes in male/female ratio due to male-biased harvest may alter rates of pregnancy, timing of parturition, and synchrony of parturition if inadequate numbers of males are present to fertilize females during their first estrous cycle. If rates of pregnancy or parturition are influenced by decreased male/female ratios, recruitment may be reduced (e.g., fewer births, later parturition resulting in lower survival of fawns, and a less synchronous parturition that potentially increases susceptibility of neonates to predation). Our objectives were to compare rates of pregnancy, synchrony of parturition, and timing of parturition between exploited mule deer populations with a relatively high (Piceance, CO, USA; 26 males/100 females) and a relatively low (Monroe, UT, USA; 14 males/100 females) male/female ratio. We determined rates of pregnancy via ultrasonography and timing of parturition via vaginal implant transmitters. We found no differences in rates of pregnancy (98.6% and 96.6%; $z = -0.821$; $P = 0.794$), timing of parturition (estimate = 1.258; SE = 1.672; $t = 0.752$; $P = 0.454$), or synchrony of parturition ($F = 1.073$ $P = 0.859$) between Monroe Mountain and Piceance Basin, respectively. The relatively low male/female ratio on Monroe Mountain was not associated with a protracted period of parturition. This finding suggests that relatively low male/female ratios typical of heavily harvested populations do not influence population dynamics because recruitment remains unaffected.

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KEY WORDS male/female ratio, mule deer, *Odocoileus hemionus*, rates of pregnancy, sex ratio, synchrony, timing of parturition, ungulate management.

The exploitation of ungulates potentially alters characteristics of populations such as sex ratio, age structure, population size, and genetic variation (Langvatn and Loison 1999, Strickland et al. 2001, Patterson and Power 2002, Festa-Bianchet 2003, Allendorf et al. 2008). For example, limiting male harvest of Colorado, USA, mule deer (*Odocoileus hemionus*) populations on a statewide basis resulted in increased adult male/female ratios, indicating that a greater proportion of adult males (relative to younger age classes) had previously been harvested (Bishop et al. 2005, Bergman et al. 2011). In a population of Norwegian moose (*Alces alces*), 70% of males were harvested before 3 years of age (Solberg et al. 2002). Both examples indicated that a portion of the population was preferentially harvested, resulting in a

sex-age structure that was skewed when compared with unharvested populations. Similarly, males with large horns or antlers are preferentially harvested from many populations, potentially removing genetic variation coding for these traits (Coltman et al. 2003, Allendorf et al. 2008, Monteith et al. 2013). Because harvest of most ungulate populations is male-biased, sex ratios are often skewed toward females (Ginsberg and Milner-Gulland 1994). This common scenario is typified for mule deer in Utah, USA, where estimated male/female ratios range from 6 to 28 males/100 females across most management units (except a few with relatively limited harvest where male/female ratios are as high as 60:100), signifying a major shift from a sex ratio at birth, which is close to 50:50 (Bernales et al. 2011).

Changes in male/female ratio have the potential to impact population dynamics (Milner et al. 2006). For example, increasing the proportion of females in a population generally increases the reproductive capacity of that population as long as there are adequate numbers of males

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for breeding (Caughley 1977). In contrast, an increase in the proportion of adult males may lower recruitment into the population because males can use resources that would otherwise be available to females and young. An increase of 4.5 males/100 females coincided with a decrease of 7.5 fawns/100 females in a population of Colorado mule deer (Bishop et al. 2005). In extreme scenarios, when sex ratios become highly skewed toward females, reduced access to mates can result in an increased proportion of females that either do not become pregnant or are bred during their second estrous cycle. Conceptually, this phenomenon is referred to as mate limitation under the Allee effect, wherein the low density of one sex results in fewer encounters with receptive mates (Courchamp et al. 1999). Therefore, heavily female-biased sex ratios can lead to fewer fawns and a less synchronous parturition period (White et al. 2001).

The synchrony and seasonality of parturition in ungulates developed under various evolutionary pressures that impact neonate survival (Sadleir 1969, Ims 1990). Variance in survival resulting from timing and/or synchrony of parturition may result from weather and food availability (seasonality in climate) or predation on newborns (Rutberg 1987, Mysterud et al. 2002). For example, timing of parturition for populations in temperate regions typically corresponds with increased resource availability to allow for sufficient growth of juveniles before the onset of harsh weather or nutritional shortage (Bunnell 1980, Clutton-Brock et al. 1982). Therefore, an extended birthing season may subject late-born neonates to environmental or nutritional conditions that are less than optimal. Supporting this assertion, individuals born later in the season often have lower survival (Clutton-Brock et al. 1987) or delayed development of body mass (Holand et al. 2003, Saether et al. 2003), causing reduced survival and lower population sizes.

Similarly, in species where predation is a major cause of mortality among neonates (e.g., mule deer), greater synchrony of parturition often results in increased survival of neonates (Sinclair et al. 2000). Although there are several ways in which synchrony of parturition can impact juvenile survival, a predator swamping effect is the best documented consequence that synchrony has on juvenile ungulates (Rutberg 1987). For example, wildebeest (*Connochaetes taurinu*) neonates born at the peak of the parturition period are more likely to survive than those born earlier or later (Estes 1976). Neonates are highly vulnerable for only a short time after birth and if parturition is condensed, vulnerable neonates are only available to predators for a limited time (Whittaker and Lindzey 1999, Testa 2002). However, if parturition is drawn-out, susceptible neonates are available for a longer time period, resulting in increased predator-related mortality. Therefore, changes in rates of pregnancy and timing/synchrony of parturition, potentially caused by an altered sex ratio, may influence neonate survival, and population growth (White et al. 2001).

Populations of mule deer are extensively exploited and have fluctuated over the past several decades with a decreasing

trend across much of western North America. Proposed mechanisms for declines include predation, severe weather, vehicle collisions, and habitat destruction (Ballard et al. 2001). Whereas research examining these causes of mule deer decline has increased in recent years, evaluations of the impacts of harvest or management strategies used to mitigate these and other factors affecting mule deer populations remain relatively rare (Festa-Bianchet 2003). Therefore, evaluating mechanisms whereby specific management strategies (e.g., increasing herd production, average age, etc.) may influence population growth can improve the effectiveness of management actions.

Our objective was to determine the influence of relatively low male/female ratios on rates of pregnancy, timing of parturition, and synchrony of parturition. Specifically, we evaluated these metrics in 2 populations with differing sex ratios. If the hunting-induced alteration of male/female ratios reduces access to mating partners enough to reduce the percentage of females that are bred during their first estrus cycle, then we would expect that pregnancy rates would be lower, dates of parturition would be later, and variance among dates of parturition would be greater in the population with a lower male/female ratio. If rates of pregnancy decrease, timing of parturition is altered, or synchrony of parturition is decreased in a population with lower male/female ratios, we will conclude that managing populations for increased production has unintended, indirect impacts that negatively influence population dynamics.

STUDY AREA

We selected 2 study areas to enable a comparison between mule deer populations. Monroe Mountain was located in south-central Utah (39°10'–39°46'N latitude) and was managed by the Utah Division of Wildlife Resources as general season unit 23. During December 2011 the Monroe Unit had one of the lowest male/female ratios in the state of Utah—14 males/100 females. The Piceance Basin was located in western Colorado and was managed by Colorado Parks and Wildlife as game management unit 22 (GMU 22; 39°48'–40°08'N latitude), which was within data analysis unit 7 (DAU 7). The sex ratio estimate for this area of Colorado was 26 males/100 females in December of 2011. Although these are not extreme sex ratios, these populations were representative of the low and high end of the general spectrum found in exploited populations. These estimates of male/female ratios were obtained from samples taken on the winter range found in our study areas. Biologists with extensive experience classifying these specific populations (>5 yr for 2 observers in both study areas) conducted helicopter or ground surveys during the mule deer rut (late Nov–early Jan) and classified all individuals that they encountered as fawns, females, or males. Classifications are done during this time because males and females are together and sightability is likely most similar for the 2 sexes (Stent 2011). In Utah, 1,468 individuals were classified and the estimated population size was 6,800 (21.6%). In Colorado DAU 7, 7,894 individuals were classified from an estimated population size of 45,000–50,000 individuals

(approx. 16.6%). Population size was not estimated for GMU 22 (a segment of DAU 7), but 534 individuals were classified within GMU 22 boundaries. Land ownership in both study areas was divided between federal agencies (Forest Service and Bureau of Land Management), state lands, and private land-holdings. Vegetation types were similar for both study sites and included areas dominated by sagebrush (*Artemisia tridentata*), serviceberry (*Amelanchier alnifolia*), mountain mahogany (*Cercocarpus ledifolius*), piñon pine (*Pinus edulis*), juniper (*Juniperus osteosperma*), Gambel oak (*Quercus gambelii*), aspen (*Populus tremuloides*), and several conifer species (e.g., ponderosa pine [*Pinus ponderosa*], Douglas-fir [*Pseudotsuga menziesii*]).

METHODS

In March 2012, we captured female mule deer (via helicopter net-gunning; Barrett et al. 1982, Krausman et al. 1985, White and Bartmann 1994) at both study areas (Fig. 1). At each study area, captures were conducted at 4 separate regions of winter-range to ensure our samples were dispersed and comparable. For each female captured, we determined pregnancy via trans-abdominal ultrasonography (E.I. Medical Imaging, Loveland, CO; Smith and Lindzey 1982). We fitted pregnant females with very high frequency radiocollars (Telonics, Mesa, AZ; and Advanced Telemetry Systems, Inc., Isanti, MN) and vaginal implant transmitters (VIT; Advanced Telemetry Systems, Inc.). We inserted VITs, using a vaginoscope, until the antennae protruded ≤ 2 cm from the female's vagina. We also assessed body size (hind foot length, chest and neck girth), condition (body condition score method; Cook et al. 2007, 2010), and age (estimation based on tooth wear and eruption pattern; Severinghaus 1949, Robinette et al. 1957) of each captured individual prior to release.

Between the original capture and parturition, we located collared females using radiotelemetry. During March and April, individuals were located sporadically from the ground or a fixed-wing aircraft. In early May, we attempted to locate every female twice per week. Beginning the last week of May, we located each female at least every other day, continuing until every VIT had been expelled.

When an expelled VIT was detected (pulse rate was doubled; 80 pulses/min), we located the VIT, determined whether it was expelled at a birth site, and recorded a date of parturition for that individual. Because some VITs are expelled prior to parturition (Bishop et al. 2011), we included only those parturition dates where VIT expulsion was corroborated by additional evidence (i.e., birth site identification and observation of neonates or females). We identified birth sites using a suite of characteristics indicative of parturition (e.g., matted down vegetation, blood, and the remains of afterbirth; Bishop et al. 2011). We also attempted to locate the parturient female, observed her behavior and body condition, and determined whether she was still pregnant. As part of a larger study, we captured and collared fawns associated with VITs that had been expelled. This corroborative evidence allowed us to confirm what day a fawn was born (based on hoof growth, wet pelage, distance from birth site, and condition of the umbilicus; Haugen and Speake 1958, Robinette et al. 1973, Sams et al. 1996, Lomas and Bender 2007).

We used pregnancy testing and parturition dates obtained from females at both study sites (Monroe and Piceance) to compare rates of pregnancy and timing and/or synchrony of parturition. We utilized a z -test of proportions to compare rates of pregnancy and a Levene's test to compare within-year variance of parturition dates between sites. Each of these tests was performed using the 1-tailed hypothesis that mule deer from Piceance (the area with a higher male/female ratio) should have higher pregnancy rates and a more synchronous parturition period. We used a general linear model to evaluate potential differences in timing of parturition. Our model included the population of origin, age, and body condition of each individual as explanatory variables for the date of parturition. This approach allowed us to account for factors (age and condition) that potentially affect date of parturition. Whereas we report calendar dates for ease of interpretation, these analyses were performed using Julian dates. Additionally, to enable a comparison to previous documentation of mule deer parturition, we computed the percentage of births that occurred in an 18-day period (Bowyer 1991).



Figure 1. Map of the United States of America with an inset showing the locations of the study populations in the Intermountain West. The Monroe Mountain, Utah location is represented as a filled circle and the Piceance Basin, Colorado location as a filled square. Dates of parturition for mule deer (*Odocoileus hemionus*) were collected from each site in 2012.

RESULTS

We captured 69 female mule deer at Monroe Mountain, Utah and 120 female mule deer at Piceance Basin, Colorado. Ultrasonography revealed that 68 of 69 (98.6%) of the Monroe females and 116 of 120 (96.7%) of the Piceance females were pregnant. These rates of pregnancy were not different between populations ($z = -0.821$; $P = 0.794$).

We obtained dates of parturition for 36 females in the Monroe population and 58 females in the Piceance population. This reduced sample was the result of mortality, extended migration, collar failure, difficulty locating some expelled VITs in a timely manner, and uncertainty concerning whether some VITs were expelled at parturition (making parturition estimates for these individuals unsuitable or unreliable; criteria for this determination are described in Methods Section). Dates of parturition in the Monroe population occurred between 1 June and 30 June ($\bar{x} = 13$ Jun, $SE = 1.00$ days) and in the Piceance population between 31 May and 12 July ($\bar{x} = 10$ Jun, $SE = 1.02$ days). Both distributions demonstrated a slight positive skew (Fig. 2). We found no difference in timing of parturition between the 2 populations (estimate = 1.258, $SE = 1.672$, $t = 0.752$, $P = 0.454$; Fig. 2).

Variance (a measure or surrogate for parturition synchrony) was 37.0 ($SD = 6.1$ days) in the Monroe population and 60.2 ($SD = 7.8$ days) in the Piceance population. Using a Levene's test, we found no difference in the variance among dates of parturition between the 2 populations ($F = 1.073$ $P = 0.859$; Fig. 2). Likewise, 91.6% of the births that we detected in the Monroe population and 89.8% of the births that we detected in the Piceance population occurred in an 18-day period.

DISCUSSION

Rates of pregnancy did not differ between populations with relatively high and low male/female ratios. This finding

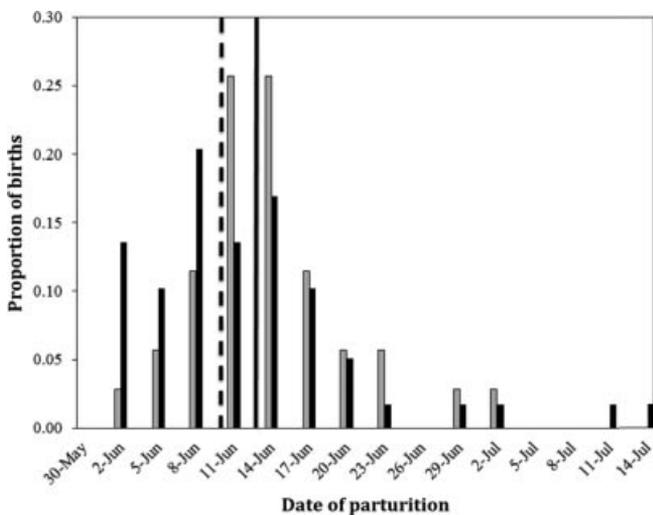


Figure 2. Proportion of births by mule deer (*Odocoileus hemionus*) that occurred during each 3-day period of the 2012 parturition season. Grey bars illustrate parturition from a population with 14 males:100 females ($SD = 6.1$; Monroe, UT, USA) and black bars illustrate parturition from a population with 26 males:100 females ($SD = 7.8$; Piceance Basin, CO, USA). Mean dates of parturition are represented as solid and dashed lines, respectively.

indicates that mate limitation under the Allee effect (which implies that reproduction is decreased because the density of individuals of the opposite sex is not high enough) is not occurring at the male/female ratios that we sampled and most adult females in both populations had mating opportunities. We performed ultrasounds in early March; therefore, it is also possible that a higher percentage of females (than we documented) were originally impregnated (Robinette et al. 1955). The rates of pregnancy in both populations are well within, or greater than, the range of variation that has been previously documented for mule deer. Examples include 93% pregnancy in each of 2 Colorado populations (Andelt et al. 2004, Bishop et al. 2009) and 94% in a Utah population (Robinette et al. 1955). Additionally, the high fertilization rates that we observed are consistent with reports from other harvested populations of ungulates (Mysterud et al. 2002). Whereas rates of pregnancy are pertinent and important, females being bred during their second estrous cycle would still have been classified as pregnant. If this occurred with greater frequency in the population with a lower male/female ratio, parturition would likely be later in the year and less synchronized.

Timing of parturition has evolved to maximize fitness (Sadleir 1969). The peak of the birthing season should be early enough in the year to allow juveniles to build sufficient fat stores for the coming winter (limiting the impact of abiotic conditions) and concurrent with the period of greatest resource availability so as to support lactating females (Millar 1977, Robinette et al. 1977, Rutberg 1987). Low male/female ratios may elongate or delay the birthing season if a decreased proportion of females are fertilized during their first estrous cycle, potentially reducing the survival of late-born fawns (Clutton-Brock et al. 1987). We found no difference in mean timing of parturition between populations with a relatively high and low male/female ratio, suggesting conception for the majority of deer in the first estrous cycle, regardless of male/female ratio. Both of the mean dates of parturition that we observed fell within the range of reported variation (early Jun–late Jul; gestation averages 203 days) for populations in the western United States (Robinette et al. 1977, Bowyer 1991, Lomas and Bender 2007, Long et al. 2009). In contrast to our analyses of free-ranging populations, a statistically significant difference existed between mean dates of parturition (4–5 days earlier with higher male/female ratio) in a comparison of captive caribou (*Rangifer tarandus*) populations (Holand et al. 2003). Although a variety of factors influence date of parturition, we have either accounted for these factors (age and condition) or there are not large differences between the 2 populations (latitude, climate, vegetation type, etc.; McGinnes and Downing 1977, Rachlow and Bowyer 1998).

Synchrony of parturition was not influenced by male/female ratio (as demonstrated by the lack of difference in the variance of parturition dates between populations). This lack of difference indicates that most females were bred during their first estrous cycle, resulting in a highly synchronized period of parturition. If most females were not bred during their first estrous cycle we would expect to see multiple

distinct peaks in our dates of parturition data. Similar to our findings, 80% of births in a California, USA, mule deer population and 95% of captures of mule deer neonates in a different Colorado population occurred in an 18-day period (Bowyer 1991, Pojar and Bowden 2004). Additionally, standard deviations for periods of parturition that have been previously published include 7.4 days in California (Bowyer 1991), 7.3 in Oregon, USA (Long et al. 2009), and 6.9 days in Washington, USA (Steigers and Flinders 1980), which are comparable to our results. Observations of a captive caribou population resulted in similar conclusions—no difference in synchrony of parturition between higher and lower male/female ratios (Holand et al. 2003). The lack of difference in synchrony of parturition that we observed indicates that relatively low male/female ratios likely do not reduce population growth through increased predation resulting from an elongated time-period when susceptible neonates are available (Estes 1976, Rutberg 1987).

We recognize that there are other means by which male harvest or skewed male/female ratios may influence populations. For example, genetic diversity may decrease as a large proportion of males or males with specific traits are harvested (Coltman et al. 2003). Additionally, when the proportion of males is decreased, younger individuals may participate more actively in the rut. The relatively few remaining males may then invest more energy to fertilize all available females (Saether et al. 2003). These changes have the potential to result in increased energy expenditure and decreased body mass for males in a population (Solberg and Saether 1994).

Examinations of the mechanisms by which low male/female ratios are theorized to decrease fawn/female ratios are lacking. Our data provide empirical evidence that was previously unavailable, suggesting that there is not a correlation between observed male/female ratios and rates of pregnancy or timing and/or synchrony of parturition in mule deer populations. We recognize that additional years and populations (with a greater range of male/female ratios) would strengthen our analysis, but these data are costly to collect and unavailable. The advent of VITs has improved our ability to accurately identify dates of parturition, allowing for comparisons that were previously unavailable or anecdotal. Our data support previous assertions that relatively low male/female ratios are not affecting recruitment in mule deer populations. For example, lower male/female ratios were not correlated with decreased fawn/female ratios during the winter after birth, indicating that low male/female ratios were not negatively affecting fawn survival (Bishop et al. 2005, Bergman et al. 2011). Although data that describe synchrony of parturition are available for many species (including mule deer), no comparative data exist between free-ranging populations with differing sex ratios.

MANAGEMENT IMPLICATIONS

There was no difference in rates of pregnancy or synchrony of parturition between populations with different male/female ratios. The relatively low male/female ratios typical of heavily harvested populations do not appear to influence population

dynamics via rates of pregnancy or synchrony of parturition. Whereas some populations have male/female ratios as high as 60:100, the range of variation that we tested (14–26 males/100 females) is representative of many, if not most, harvested populations. Increasing male/female ratios above 14 males/100 females should not be used as a management strategy for increasing rates of pregnancy or for modifying the timing and/or synchrony of parturition.

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