



*Special Section on Mountain Sheep Management*

# Horn Size and Nutrition in Mountain Sheep: Can Ewe Handle the Truth?

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**ABSTRACT** Horns, antlers, and other horn-like structures are products of sexual selection, confer reproductive advantages, and are heritable and honest indicators of individual quality. In addition to serving key biological functions, horns and antlers garner societal interest that, when combined with the powerful motivation to acquire trophy animals, likely has spawned a growing hornographic culture fixated on males with exceptional horn-like structures. The concern that harvest of large, fast-growing males may cause evolutionary change to the very trait being sought has been the source of controversy in the popular and scientific literature over the past 2 decades. Mountain sheep (i.e., bighorn and thinhorn; *Ovis* spp.), possibly the only large ungulates in North America managed almost exclusively as trophy species throughout their ranges, embody this controversy, which has led to polarizing views among scientists and stakeholders as to how mountain sheep should be managed. Our goal in this commentary was to discuss the relative contributions of the key ecological and intrinsic factors that influence horn growth, how those factors might interact with harvest strategies, and identify what determinants of horn size are most amenable to management and most effective in achieving desired outcomes. Despite repeated results demonstrating that age or nutrition frequently override genetic contributions to size of horns, attention has been given to the role of genetics and its relationship to harvest of mountain sheep. Given the hyperbole surrounding trophy management and big horns, we suggest the importance of females in the management of mountain sheep has been largely forgotten. Maternal condition can instigate life-long effects on size and growth of males (via maternal effects), and abundance of females, in turn, affects nutritional limitation within populations through density-dependent feedbacks. If production of males with large horns is an objective, we contend that management programs should, integrate monitoring of nutritional status of populations, and where evidence indicates nutritional limitation through density dependence, seek to regulate abundance and per capita nutrition via harvest of females. We propose that extrinsic regulation (i.e., removal by harvest or translocation) is the most effective way to manage per capita availability of forage resources and, thus, nutritional limitation on growth of males. Not only can female harvest improve growth in body size and horns of males through enhanced nutrition of growing males and their mothers, such management also 1) may yield a nutritional buffer against environmental stochasticity and erratic population fluctuations, 2) be employed in areas where other management alternatives such as habitat manipulation may not be feasible, 3) may reduce frequency or magnitude of epizootic die-offs, and 4) will increase hunter opportunity and involvement in management. Ultimately, we call for greater recognition of the pervasive role of the ewe, and other female ungulates, in the production of trophy males, and that accordingly, females be better integrated into harvest and management programs. © 2017 The Wildlife Society.

**KEY WORDS** antler size, density dependence, female harvest, maternal effects, *Ovis canadensis*, *Ovis dalli*, selective harvest, trophy hunting.

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The kingdom Animalia is replete with examples of status symbols and elaborate structures among males (Emlen 2008). Those adornments are as diverse as they are fascinating (Geist 1966a, Emlen 2008), and include examples such as the branched horn of the rhinoceros beetle (*Trypoxylus dichotomus*), which can reach two-thirds of its

body length (McCullough and Emlen 2013); the solid keratin horn of the white rhinoceros (*Ceratotherium simum*), which can exceed 1.5 m in length (Player 1972); the unwieldy and legendary antlers of the extinct Irish elk (*Megaloceros giganteus*), which spanned >3 m (Gould 1974); the horns of the pronghorn (*Antilocapra americana*), which are uniquely branched and deciduous (Bubenik and Bubenik 1990); and the heavy, spiraling horns of bighorn sheep (*Ovis canadensis*), which can exceed 12% of body mass (Geist 1966b). These and other similar structures are a product of sexual selection (Jarvi et al. 1987, Andersson 1994), and are used to bolster reproductive success by attracting females, intimidating rival males, and conferring an advantage in male–male combat.

Some of the best-studied adornments in the animal kingdom are the pronghorns, antlers, and horns possessed by antilocaprids, cervids, and bovids, respectively (order Cetartiodactyla). Sexual selection presumably has favored the development of large structures in those taxa as a result of the reproductive advantages they confer (Andersson 1994, Bro-Jorgensen 2007). Indeed, size and symmetry of those structures are heritable traits (Williams et al. 1994, Kruuk et al. 2002, Coltman et al. 2003), and are considered to be honest signals of phenotypic quality (Solberg and Sæther 1993, Ditchkoff et al. 2001, Vanpe et al. 2007, Bonenfant et al. 2009b). Males with large horns or antlers often produce more or better sperm (Malo et al. 2005), are more resistant to parasites (Ezenwa and Jolles 2008), have greater body mass (Festa-Bianchet et al. 2004, Monteith et al. 2009), and enjoy enhanced reproductive success (Coltman et al. 2002, Kruuk et al. 2002, Preston et al. 2003) compared with small males.

Despite increased reproductive success conferred by large horns or antlers, their growth is costly and demands resources beyond those needed for maintenance, or growth in body size. Allocation of resources to growth of those structures is tied to aspects of the environment that affect the nutritional condition of an individual (Festa-Bianchet et al. 2004, Monteith et al. 2009, Michel et al. 2016b). All else being equal, males in the best physical condition have the ability to allocate more resources to the production of horns or antlers than males that are in poor physical condition (Simmons and Emlen 2006, Emlen et al. 2012). Consequently, elaborate structures are not only of value in male–male combat but are a conspicuous signal of individual prowess and overall quality to rivals and potential mates (Geist 1971). Indeed, the assessment of a rival male through honest signals in weaponry may allow individual contests to be resolved without dangerous battles (Barrette and Denis 1986), and allows females to assess the quality of potential mates (Zahavi 1975; Zahavi and Zahavi 1997; Bowyer et al. 2007, 2011).

In addition to playing key roles in reproduction and behavior of wild animals, horns and antlers captivate imaginations, adorn walls, and provide millions of dollars in funding for conservation and management programs worldwide. Animals with exceptionally large horns or antlers adorn the glossy covers of popular magazines and advertisements (Messner 2011), reflecting a culture of hornography where the acquisition of trophy animals has become, for

some, a powerful motivation (Damm 2008, Knox 2011, Messner 2011, Heffelfinger 2016, Simon 2016). In some instances, recreational hunters pay large sums of money to increase the opportunity to harvest a large specimen, whether through the hiring of an outfitter or guide, or through the purchase of a highly coveted permit (Erickson 1988, Whitfield 2003, Festa-Bianchet and Lee 2009, Festa-Bianchet 2012b, Palazy et al. 2012). Funds generated through the sale or auction of special opportunity permits have been a boon for wildlife conservation across much of the world (Lindsey et al. 2007, Becker et al. 2013). Auction of permits to fund conservation programs for mountain sheep (e.g., Rocky Mountain bighorn [*Ovis canadensis canadensis*], desert bighorn [*O. c. nelsoni*]), Dall's [*Ovis dalli*]) have yielded millions of dollars, and have produced >\$400,000 for a single permit (Landers 2013).

Perhaps as a consequence of the growing interest in large horns and antlers, management of some species has become focused on the production of trophy-sized animals (Damm 2008, Knox 2011, Chitwood et al. 2015). Mountain sheep may well represent the only large ungulates in North America that are managed almost exclusively as trophy species throughout their ranges. Nonetheless, side-effects of marketing associated with the sales of fund-raising tags (e.g., further emphasis on trophy harvest and the appearance of commercialization of wildlife) have been a source of controversy (Damm 2008, Festa-Bianchet 2012b, Simon 2016, Heffelfinger 2017).

Given the biological, sociological, and economic value of horns and antlers, a firm understanding of the factors that influence their growth is of fundamental importance. A misunderstanding of the relative contributions of various factors to growth, particularly in mountain sheep, has been the source of debate and confusion in the popular and scientific literature over the past decade. This debate has led to polarizing views between scientists and stakeholders about how mountain sheep should be managed and, specifically, how current harvest practices contribute to the growth and size of horns. Indeed, realizing management objectives is contingent upon knowing how our actions or strategies affect size, whether intentionally or unintentionally. Our goal in this commentary is to discuss the relative contributions of key ecological and individual-based factors that influence horn growth, how those factors interact with harvest strategies, and to identify what determinants of horn size are most amenable to management and most effective in achieving desired outcomes.

### **The Trifecta: Age, Genetics, and Nutrition**

Growth and size of horns and antlers are determined primarily by 3 factors: age, genetics, and nutrition (Goss 1983, Bubenik and Bubenik 1990). The relative contributions of each factor, however, are not equal, and in many instances their effects are interactive.

Heritability, a metric of the degree of similarity between relatives with regard to specific traits, indicates how sensitive a trait is to selective pressures acting on that trait (Brookfield 2009). Size and configuration of horns and antlers is, at least

in part, heritable (Williams et al. 1994, Lukefahr and Jacobson 1998, Kruuk et al. 2002); however, reported estimates of heritability for size and configuration vary (Michel et al. 2016a). For example, Coltman et al. (2003) estimated heritability of horn length in bighorn sheep to be 0.69 (i.e., the proportion of variability among individuals of genetic origin), although this estimate for the same population was more recently estimated at 0.39 (Pigeon et al. 2016). Similarly, estimates of heritability in antler traits in red deer (*Cervus elaphus*) have ranged from high (0.81; Ward et al. 2014) to modest heritability (0.35; Kruuk et al. 2002). When all else is equal, given the heritability in these traits, sons sired by males with large horns or antlers tend to possess larger horns or antlers than those sired by males with smaller horn-like structures. Moreover, there exists some level of concordance among phenotypic traits and other life-history characteristics, such as body size and maternal performance (Coltman et al. 2005, Poissant et al. 2008). Covariance among life-history and phenotypic traits, however, also may result from other factors such as nutritional condition (Mousseau and Roff 1987, Rowe and Houle 1996), and likely explains at least some of the variation in heritability of horns or antlers observed among studies and ecosystems (Michel et al. 2016a). Heritability is an important consideration in management programs, because management actions that target a heritable phenotypic trait, especially one that is linked to fitness, can have important implications for growth and other life-history traits (Poissant et al. 2008, Myrsetrud 2011).

Among artiodactyls, pronghorn, chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), and mountain goats (*Oreamnos americanus*) are exceptions because they can attain peak horn size at 2 or 3 years of age (Mitchell and Maher 2006, Festa-Bianchet 2012a); otherwise, older age generally is necessary for development of large horns or antlers. Among cervids, which annually grow and shed antlers, peak antler size typically is not achieved until growth in body size is complete, which can occur from 6 to 12 years of age depending upon the species (Stewart et al. 2000, Bowyer et al. 2001, Bender et al. 2003, Monteith et al. 2009). In contrast, among bovids, the size of true horns reflects an accumulation of seasonal growth throughout the life of an individual and, therefore, peak size is attained at maximal age (Hoefs and Nowlan 1997, Loehr et al. 2007, Bergeron et al. 2008). Thus, only with brooming (the loss of horn as a result of wear) or breakage does size of horns become smaller as an animal grows older (Shackleton and Hutton 1971). Nevertheless, male mountain sheep can attain nearly 80% of their peak horn length by 5 years of age (Hoefs and Nowlan 1997, Jorgenson et al. 1998) and the rate of increase in horn length can peak as early as age 2 (Hemming 1969, Bonenfant et al. 2009b). Additionally, rate of increase in horn volume typically peaks at 4 or 5 years of age (König and Hoefs 1984, Loehr et al. 2007). Although fast-growing males reach larger sizes more rapidly than slower-growing males, horn size is a terminal trait (manifests at max. age) and, consequently, age is an important determinant of horn growth and size. Therefore, age structure plays a critical role in determining

the distribution of horn sizes within a population. Among populations of artiodactyls, age structure of males can be associated closely with level of harvest (Jenks et al. 2002) and, consequently, sufficient harvest pressure can reduce the size of animals available for harvest by lowering the age structure of a population (Monteith et al. 2013a).

Large ungulates are long-lived, iteroparous mammals and, consequently, exhibit a conservative life-history strategy wherein survival typically is favored over allocation to reproduction (Martin and Festa-Bianchet 2010, Monteith et al. 2013b). Among male ungulates, allocation of resources to reproduction corresponds with allocation to growth of horns, antlers, and body size (Coltman et al. 2002), and sometimes costly changes in behavior that take place during the mating season (Willisch and Ingold 2007, Myrsetrud et al. 2008). Growth of horns or antlers requires resources beyond those necessary for basic metabolic needs (Bubenik and Bubenik 1990, Monteith et al. 2009, Rands et al. 2011), which results in an implicit tradeoff. As expected from sexual-selection theory, large horns or antlers typically increase reproductive success of mature males (Clutton-Brock 1982, Coltman et al. 2002, Preston et al. 2003, Malo et al. 2005, DeYoung et al. 2006); however, in some species reproduction is unrelated to weapon size and alternative mating strategies can weaken benefits of large weapons (Hogg 1984, Mainguy et al. 2008, Festa-Bianchet 2017). Horns and antlers are not critical for survival, especially when compared with body growth or maintenance of body stores. Thus, young males prioritize physical development over growth in horn-like structures (Festa-Bianchet et al. 2004, Michel et al. 2016b, Douhard et al. 2017), a situation analogous to that of females in which maintenance takes precedence over allocation of resources to reproduction or growth of young (Monteith et al. 2009, Martin and Festa-Bianchet 2010). As a result, nutritional status of populations plays a critical role in growth of those costly structures.

### **Nutrition: A Fundamental Mechanism**

In seasonal and unpredictable environments, where food availability can fluctuate, females should ensure that they retain sufficient body reserves to survive food-limited periods by reducing reproductive output accordingly (Therrien et al. 2008, Bårdsen et al. 2011). When maternal nutrition is compromised, young are smaller at birth (Keech et al. 2000, Monteith et al. 2009), nursing and maternal care decline (Rachlow and Bowyer 1998, Therrien et al. 2007, Scornavacca et al. 2016), growth of young is suppressed (Festa-Bianchet and Jorgenson 1998, Martin and Festa-Bianchet 2010, Tollefson et al. 2011), and mortality of young increases (Therrien et al. 2007, Monteith et al. 2014, Scornavacca et al. 2016). This conservative life-history strategy transfers the costs of reproduction from females to their young (Festa-Bianchet and Jorgenson 1998, Martin and Festa-Bianchet 2010, Monteith et al. 2014). Such selfish maternal tactics can have a cascading effect on the demography and dynamics of populations, all of which are mediated through maternal nutrition.

There are 2 primary pathways by which nutrition can affect growth and, ultimately, size of horn-like structures: maternal effects and direct environmental effects. A maternal effect is the direct influence of the phenotype of the mother on the phenotype of her offspring, and is unrelated to the genes that the offspring inherits (Bernardo 1996, Reinhold 2002). Specifically, offspring phenotype depends on the genes inherited from the mother and father, but mothers also affect offspring size by their ability to provision the resources needed for growth and development, an ability that is dependent upon the nutritional landscape (Therrien et al. 2007, Bårdsen et al. 2008, Tollefson et al. 2011, Monteith et al. 2013b, Long et al. 2016). Maternal effects have been recognized, but often are an underappreciated or unmeasured factor in animal ecology. Nevertheless, the conservative life-history strategy of long-lived, iteroparous species, when combined with an extended period of maternal care, makes those taxa prime candidates for maternal effects to manifest (Reinhold 2002).

Condition-dependent allocation of maternal resources to offspring can result in a negative maternal effect that can compromise growth of offspring and prevails through adulthood, regardless of whether improved conditions occur later in life (Albon et al. 1987, Mech et al. 1991, Lindström 1999, Monteith et al. 2009, Thalmann et al. 2015). Moreover, failure to adequately account for maternal effects and other nutritional contributions to growth can yield overestimates of additive genetic variance and, therefore, inflated estimates of heritability (Milner et al. 2000, Wilson et al. 2005). Indeed, directional selection often fails to result in an evolutionary response, even when heritability of traits was high (Milner et al. 1999; Kruuk et al. 2001, 2002; Michel et al. 2016a). Intergenerational maternal effects on offspring phenotypes highlight the importance of maternal nutrition and demonstrate a likely mechanism for cohort effects (Monteith et al. 2009), which are frequently observed in ungulate populations (Albon et al. 1987, Andersen and Linnell 1997, Rose et al. 1998, Nussey et al. 2005, Hamel et al. 2016).

Conservative allocation of resources by mothers to their offspring, in combination with the environmental conditions experienced by individuals at a young age, can have a life-long effect on the ability of males to attain large body size and produce large horns or antlers, regardless of their genetic potential. With few exceptions (Festa-Bianchet 2012a), compensation for a poor start is rare, which highlights the pervasive influence of maternal and cohort effects on adult size (Toïgo et al. 1999, Festa-Bianchet 2012a, Carvalho et al. 2017). For example, in Alpine ibex (*Capra ibex*), the rate of horn growth early in life was correlated positively with horn length throughout life (Toïgo et al. 2013, Willis et al. 2015). A single year of poor nutrition early in life can have lifetime consequences for an entire cohort of males in a population (Albon et al. 1987, Rose et al. 1998, Lindström 1999, Schmidt et al. 2001, Pérez et al. 2011).

For sexually dimorphic mammals, growth and survival of males often are affected more strongly by environmental conditions than growth and survival of females (Glucksmann

1974, Rose et al. 1998, Toïgo et al. 1999). In response to resource limitation, female ungulates can postpone primiparity, reduce litter size, or both, and thereby decrease allocation of resources to reproduction to conserve those resources for themselves (McCullough 1979, Festa-Bianchet and Jorgenson 1998, Therrien et al. 2008, Monteith et al. 2014). In contrast, options for allocation of resources by males are less diverse and are focused almost entirely on growth; as a consequence, resource limitation is likely to have a more dramatic effect on size of males than on females (Hamel et al. 2016).

Until asymptotic body mass is achieved, growth in body size is prioritized over that of horns or antlers (Stewart et al. 2000, Festa-Bianchet et al. 2004, Monteith et al. 2009). Accordingly, the influence of resource limitation on growth of horns or antlers is strongest early in life, when investment in those structures competes with allocation in body mass (Jorgenson et al. 1998, Festa-Bianchet et al. 2004). When food is limited, young males may allocate relatively more resources to body growth than to horn growth, thereby trading long-term reproductive success for short-term survival (Festa-Bianchet et al. 2004, Anderwald et al. 2015). Indeed, large horns or antlers are ultimately a reproductive allocation, and the reproductive benefits of large structures are not realized until prime age (Coltman et al. 2002), although alternative mating tactics may alter this relationship (Hogg 1984, Johnson et al. 2006).

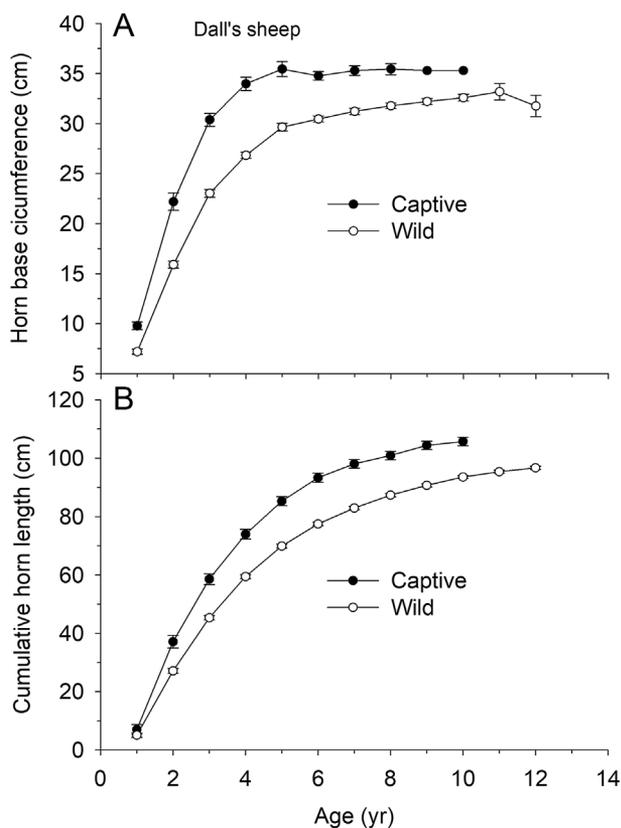
In addition to maternal allocation, resources available during early development and growth can have cumulative effects on growth and size of horns or antlers (Carvalho et al. 2017). For example, forage growth in spring, as indexed by spring precipitation, explained 86% of the variation in annual increments of horn length of Dall's sheep in a population in the Yukon (Bunnell 1978), and similarly, annual horn growth of Dall's sheep over 42 years in the Yukon was best explained by nongenetic factors associated mostly with spring-time weather (Loehr et al. 2010). Moreover, springtime temperatures across 4 decades in the eastern Swiss Alps resulted in synchronization of interannual variation in horn growth across 8 populations of Alpine ibex (Büntgen et al. 2014).

Variation in resource availability also can interact with changes in population density to influence growth of horns and antlers (Bowyer et al. 2014). For example, dramatic increases in density of a bighorn sheep population in Alberta, Canada, had strong, negative effects on annual increments of horn growth up to 4 years of age and effectively diluted potentially positive effects of spring precipitation (Jorgenson et al. 1998, Douhard et al. 2017). Resource availability throughout life, but especially during the first few years of life, influences adult size, especially for horned animals, because horns reflect a lifetime accumulation of growth, and horn produced early in life affects ultimate size of horns attained at prime age.

Sophisticated modeling techniques can be used to parse genetic, environmental, and maternal contributions to horn and antler size (Coltman 2008, Wilson et al. 2010). Nonetheless, manipulative experiments have demonstrated

the overriding influence of nutrition on growth of male ungulates by varying nutrition while controlling for the genetic contributions to growth. For example, in a common garden experiment, Monteith et al. (2009) demonstrated that conditions during gestation can have life-long consequences for growth of male white-tailed deer (*Odocoileus virginianus*), even if nutrition improves post-parturition. Male offspring born after foraging conditions were experimentally improved achieved 26% larger antler size and 30% larger body size than their sires (Monteith et al. 2009). In a similar experiment with white-tailed deer from 3 geographic regions, increases in antler size and body mass following improved foraging conditions were related inversely to the quality of the range from which the animals were initially obtained (Michel et al. 2016b).

Hoefs and Nowlan (1997) evaluated horn growth in a free-ranging population of Dall's sheep in Kluane National Park, Yukon, Canada, and that of a captive herd receiving high-quality feed that was established with animals from the Park. Although sample size was small, differences in horn growth between captive and free-ranging animals were striking (Fig. 1), despite originating from the same population and, thus, presumably having similar genetic origins. Captive

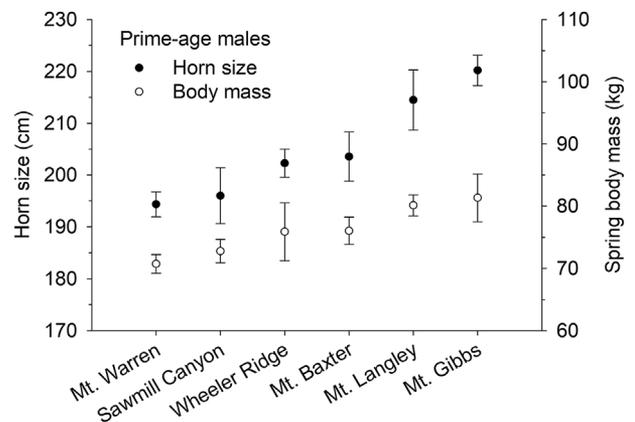


**Figure 1.** Annual circumference (cm  $\pm$  SE) of horn base (A) and cumulative length (cm  $\pm$  SE) of horns (B) relative to age for Dall's sheep that resided in Kluane National Park, southwest Yukon, Canada ( $n = 24$ ), and a captive herd that was established from animals captured from Kluane National Park ( $n = 10$ ), 1969–1992. The wild herd existed at high density, whereas the captive herd was maintained with alfalfa hay and a pelleted ration yielding superb nutrition (data adapted from Hoefs and Nowlan 1997).

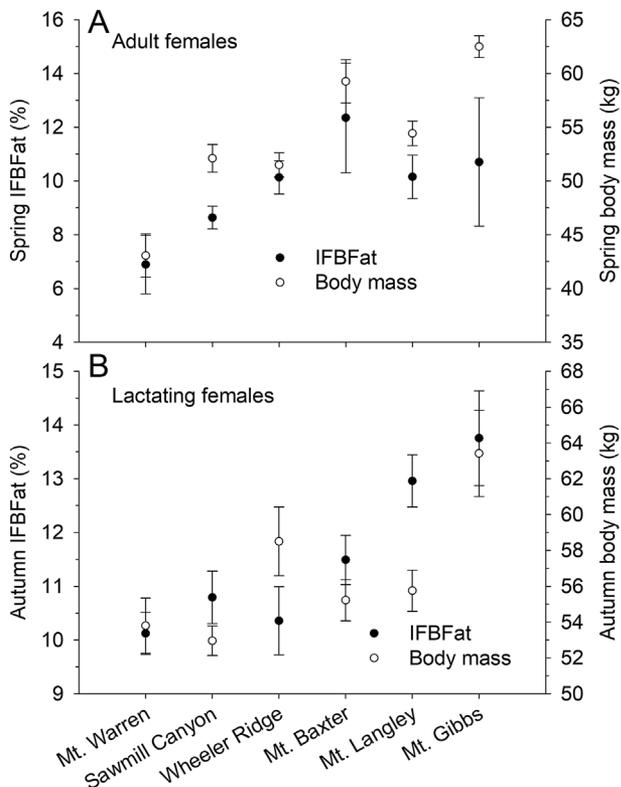
males produced horn lengths of  $>60$  cm by 3 years of age, but wild males needed 4 years to achieve that benchmark. Even more striking, wild males achieved a maximum basal circumference of 33 cm if they lived to 11 years, whereas captive males surpassed that circumference in their fourth year. Consequently, at 7 years old, overall horn size as estimated by horn volume was 57% greater for males maintained on high-quality feed when compared with their free-ranging counterparts (Hoefs and Nowlan 1997).

### A New Case Study on Nutrition and Horn Growth

The Sierra Nevada, California, USA, harbors endemic populations of an endangered subspecies of mountain sheep (*Ovis canadensis sierrae*). The absence of human harvest for this subspecies, in combination with intensive monitoring programs across multiple populations that differ in range conditions (Johnson et al. 2010), afforded a unique opportunity to evaluate relationships between nutritional status and horn size across populations (Appendix A, available online in Supporting Information). Based on data of horn size and age of males, and nutritional condition and size of females from animals captured during 2002–2016 across 6 populations in the Sierra Nevada, we evaluated associations between seasonal condition of females and age-specific horn size of males. We first estimated an age-specific index to horn size ( $n = 175$ ) as a function of age and  $\ln(\text{age})$ , with population as a fixed effect to account for differences in horn size relative to age across populations (Appendix A). Next, considering populations as our sampling units, we evaluated relationships between metrics of nutritional status (ingesta-free body fat [IFBFat] and body mass) of adult females and predicted horn size of 7-year-old males using least-squares regression weighted by the inverse of the variance of each predictor variable (Appendix A). We predicted that nutritional status of females would be related positively to age-specific horn size across populations, because nutritional status of females in spring is an indicator of the potential for direct allocation of reserves to production



**Figure 2.** Mean horn size (cm  $\pm$  SE;  $n = 65$ ) and body mass (kg  $\pm$  SE;  $n = 42$ ) in spring of male, Sierra Nevada bighorn sheep that were of prime age (6–10 yrs old) in 6 populations, 2002–2016, Sierra Nevada, California, USA. Horn size was indexed based on the sum of horn length and basal circumference for both horns.

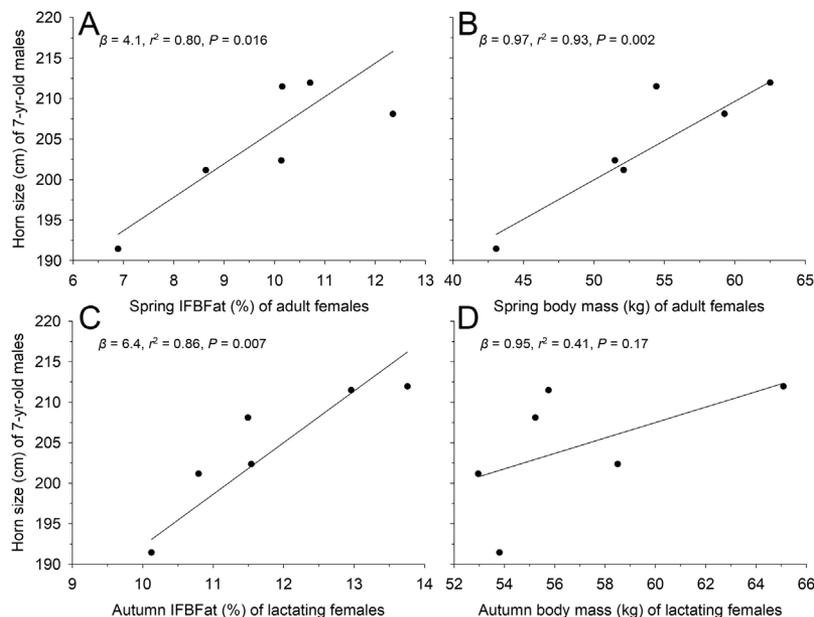


**Figure 3.** Percent ingesta-free body fat (IFBFat  $\pm$  SE) and body mass (kg  $\pm$  SE) of adult ( $\geq 2$  yrs old) female Sierra Nevada bighorn sheep ( $n=115$ ) measured during spring (A) and for lactating ( $n=96$ ) female bighorn sheep measured during autumn (B) across 6 populations, 2002–2016, Sierra Nevada, California, USA.

and growth of young, and nutritional status of lactating females in autumn is a product of range conditions during summer (Cook et al. 2013; Monteith et al. 2013b, 2014).

Mean size of horns (indexed as the sum of horn lengths and basal circumferences) of male bighorn sheep of prime-age (6–10 yrs old) ranged from 194 cm to 220 cm, and body mass in spring ranged from 71 kg to 81 kg across 6 populations in the Sierra Nevada (Fig. 2). Similarly, body mass and nutritional condition of adult females in both spring and autumn varied across populations (Fig. 3). As predicted, variation in age-specific size of horns across 6 populations, represented by predicted horn size of 7-year-old males, was correlated strongly with body mass ( $r^2=0.93$ ,  $F=50.3$ ,  $P=0.002$ ) and IFBFat ( $r^2=0.80$ ,  $F=16.4$ ,  $P=0.016$ ) of adult females in spring, and IFBFat of lactating females in autumn ( $r^2=0.86$ ,  $F=25.6$ ,  $P=0.007$ ). Horn size was not related as closely to body mass of lactating females in autumn ( $r^2=0.41$ ,  $F=2.81$ ,  $P=0.17$ ). Increasing nutritional status of adult females was associated with large increases in horn size of adult males (Fig. 4). Indeed, horn size of 7-year-old males was predicted to increase by 4 cm for every 1 percentage point increase in IFBFat or 4-kg increase in body mass of adult females in spring, and for every 0.6 percentage point increase in IFBFat of lactating females in autumn.

Nutritional condition (IFBFat) and body mass of adult females in spring explained a large proportion of the variation in age-specific horn size across populations of bighorn sheep in the Sierra Nevada (Fig. 4). Body mass of individuals is typically unrelated to nutritional condition in any 1 year because both large and small individuals can be in poor or good nutritional condition (Monteith et al. 2013b).



**Figure 4.** Predicted horn size (cm) of male bighorn sheep at 7 years old as a function of percent ingesta-free body fat (IFBFat) and body mass (kg) of adult ( $\geq 2$  yrs old) female Sierra Nevada bighorn sheep measured during spring (A, B) and autumn (C, D) across 6 populations, 2002–2016, Sierra Nevada, California, USA. Horn size was indexed based on the sum of horn length and basal circumference for both horns. Lines represent fitted least-squares regressions weighted by the inverse of the variance associated with each estimate for the predictor variable (x-axis).

Nevertheless, from the perspective of the individual, body mass is a product of long-term range conditions relative to habitat quality and feedbacks associated with density dependence (Simard et al. 2008, Monteith et al. 2009, Jones et al. 2010, Hamel et al. 2016, Michel et al. 2016*b*). Therefore, body mass yields a metric of nutritional inputs over longer temporal scales than nutritional condition. We were unable to assess nutritional condition in every herd in every year, and nutritional condition is more sensitive to interannual conditions than is body mass (Monteith et al. 2014). Consequently, we expected more variation in measures of IFBFat than in body mass and that, as a consequence, IFBFat would be less predictive of population-level differences in horn size. Nevertheless, nutritional condition of females in spring and autumn, and body mass of females in spring explained most of the variation in age-specific horn size across populations. Age-specific changes in horn size of approximately 12% across populations could be explained largely by improved nutrition (Fig. 4), and is yet another example of the pervasive effects of nutrition, and ostensibly maternal nutrition, on size of males. Indeed, physiological pathways and ecological studies in development of secondary sexual characteristics indicate heightened sensitivity to nutrition when compared with other traits, thereby reaffirming that growth and ultimate size of horn-like structures is inextricably tied to nutrition (Fig. 4; Hoefs and Nowlan 1997, Monteith et al. 2009, Emlen et al. 2012, Johns et al. 2014, Michel et al. 2016*b*).

### **The Nutritional Underpinning of Density Dependence**

Placing emphasis on the contribution of nutrition (whether maternally or environmentally mediated) to management of large ungulates requires the effective integration of nutritional principles into ecological theory and application (Monteith et al. 2014). For example, understanding population ecology of large mammals is not possible without considering density dependence, which is a life-history characteristic that is nutritionally mediated and a measurable parameter of populations (Caughley 1977, Stearns 1992, Bowyer et al. 2014). Despite the established theoretical foundations of density dependence (Bonenfant et al. 2009*a*), there remains confusion over if, and how, density dependence operates among individuals and within populations (McCullough 1979, Fowler 1981, Bowyer et al. 2014). Perhaps the greatest source of confusion stems from the widespread misunderstanding that density dependence is operating only when there are evident relationships between some metric of population performance and density. Direct and consistent relationships between measures of population performance and absolute measures of density are not always obvious; however, and this is especially so in highly stochastic environments where quantity and quality of resources varies considerably across years (Marshal et al. 2009).

The effects of resource availability via density dependence are ultimately mediated by their per capita availability, which depends on the number of individuals in a particular area (i.e., density) and on the quantity and quality of resources available to them (Monteith et al. 2014). Capacity of the

habitat to support a population varies from year to year, and from location to location; as a consequence, the degree of density dependence can be affected more by annual abundance of resources or quality of resources in the area, than by changes in density of the population itself (McCullough 1999, Monteith et al. 2014). As a result, density-dependent influences, in many instances, may go undetected and their role in populations may be underappreciated, because resource availability can change directionally or vary considerably, especially in stochastic environments (Mackie et al. 1990, Marshal et al. 2009, Pierce et al. 2012, Starns et al. 2014, Monteith et al. 2015). Given the sometimes deceptive disconnect between density and density-dependent feedbacks, understanding the role of density dependence in population dynamics and resource allocation demands data or tools that integrate density and resource abundance.

The proximity of a population to nutritional carrying capacity (short-term capacity of the environment to support population growth; Monteith et al. 2014) determines the degree of density-dependent feedbacks that individuals experience at a particular time and, thus, yields greater insight into population regulation than density itself. Vital rates of large herbivores generally respond to increasing limitation of resources in a predictable sequence, from decreased survival of young, increased age of first reproduction, decreased reproduction of adults, and lastly to decreased survival of adults (Gaillard et al. 2000, Eberhardt 2002, Bonenfant et al. 2009*a*). The underlying basis for this life-history paradigm is nutritional condition and how a long-lived, conservative mammal responds to its nutritional status (Monteith et al. 2014). When populations are near nutritional carrying capacity, intraspecific competition is intense, per capita availability of forage is low, and nutritional condition of individuals declines (Bowyer et al. 2014). Consequently, growth rate of horns or antlers is likely to be slower at higher densities than at lower densities with respect to nutritional carrying capacity because poor maternal nutrition can result in a negative maternal effect combined with limited resources available for growth of young and adult males. Among sexually dimorphic species, females compete largely with each other and young, and males compete with other males because the sexes segregate throughout much of the year (Bleich et al. 1997, Kie and Bowyer 1999, Bowyer 2004, Stewart et al. 2015). For mountain sheep, young males typically remain with female groups until 2–4 years old when they disperse to join groups of males (Geist 1971, Festa-Bianchet 1991, Bleich et al. 1997). Consequently, density-dependent effects on growth of young male sheep are expected to be most prominent during the first few years of life, which can have implications for production of horns.

### **Implications for Management of Mountain Sheep**

The combined annual harvest of Rocky Mountain bighorn sheep and desert bighorn sheep consists almost exclusively of adult males, and across the western United States averaged 2.5 males/100 individuals (range = 1.3–3.5) among hunted

populations (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008b). Harvested males represent approximately 7–12% of all males, or only 2.5% of entire populations (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008b). In stark contrast, an estimated 14.3% of deer (*Odocoileus* spp.) and 15.5% of North American elk (*Cervus elaphus*) across 19 western states and provinces were harvested in 2009 (Walker 2011). Those differences in harvest rates exemplify the status of mountain sheep as the quintessential trophy ungulate in North America. Indeed, conservative harvest rates, along with restrictions on minimum horn size or minimum age of legal animals are all designed to produce males with large horns (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008b). Ironically, the strongest evidence for evolutionary effects of selective harvest also pertains to mountain sheep, despite being managed as a trophy species (Douhard et al. 2016, Pigeon et al. 2016). This paradox has caused much debate over the management of mountain sheep, and has resulted in differences of opinion over the role of selective harvest and the genetic consequences of artificial selection imposed by hunters seeking to harvest individuals with large horns.

Evidence for selective harvest causing a genetically based reduction in horn size originated primarily from a small, isolated population of Rocky Mountain bighorn sheep at Ram Mountain, Alberta, Canada. Until 1996, harvest of male sheep was regulated only by a morphological criterion (only males having horns with a 4/5 curl were eligible for harvest), and the number of licensed hunters was not limited. Between 1973 and 1996, horn length declined by almost 30%, a trend that was partly attributed to the intensive and highly selective harvest of large, fast-growing males (Coltman et al. 2003). Indeed, 40% of the males that reached legal status were harvested each year, resulting in strong selection against males having fast-growing horns before they reached their reproductive peak (Bonenfant et al. 2009b).

Results published by Coltman et al. (2003) were, thereafter, the subject of criticism and concern over inadequate consideration of environmental effects on horn size (Heimer 2004, Festa-Bianchet et al. 2006b, Postma 2006, Coltman 2008, Traill et al. 2014). A subsequent reanalysis of those data from Ram Mountain indicated that such severe and selective harvest led to genetically based reductions in horn size, and indicated that this effect was reduced with a regulation that changed the definition of a legal sheep to full curl in 1997 (Pigeon et al. 2016). Nevertheless, under a management strategy of nearly unregulated and highly selective harvest, only 3 cm of the >15-cm reduction in age-corrected horn-length over time was attributed to genetic effects (Pigeon et al. 2016); analyses of which also have been challenged (Coulson et al. 2017). Instead, direct reductions in nutrient availability from a 2.4× increase in population abundance primarily were responsible for the phenotypic reductions in horn size (Jorgenson et al. 1993b, 1998; Wishart 2006; Pigeon et al. 2016; Festa-Bianchet 2017).

## Remembering the Forgotten Ewe

The focus on management for big horns and the genetic effects of selective harvest likely has diverted attention away from many of the other challenges faced by mountain sheep, among which are habitat loss, deterioration of habitat quality, changing climate, and epizootic respiratory disease (Risenhoover et al. 1988, Brewer et al. 2014, Jex et al. 2016, Heffelfinger 2017). Moreover, a considerable amount of attention, especially from the popular press, has been given to the role of genetics in the production of trophy animals and its relationship to harvest of mountain sheep. This outcome has occurred despite repeated demonstrations that age or nutrition frequently override genetic contributions to size of horns or antlers (Kruuk et al. 2002; Schmidt et al. 2007; Monteith et al. 2009, 2013a; Pigeon et al. 2016). Moreover, the conservative harvest regimes of most populations of mountain sheep in North America are unlikely to have genetic consequences (Festa-Bianchet 2017, Heffelfinger 2017). We do not dispute the potential for harvest to alter the frequency of alleles associated with large horns if harvest is sufficiently severe and highly selective, sufficient time has lapsed, and other selective pressures have not countered pressures associated with selective harvest (Hundertmark et al. 1998, Douhard et al. 2016, Pigeon et al. 2016, Coulson et al. 2017, Heffelfinger 2017). Instead, we contend that our intellectual and financial capital would produce greater yield by being invested elsewhere (e.g., enhancing population productivity and bolstering production of large males by improving nutritional condition of females).

Plastic changes in horn growth in response to fluctuations in quality or abundance of resources are likely to be more ubiquitous and influential than changes that are genetically based (Büntgen et al. 2014, Festa-Bianchet 2017). Therefore, placing greater emphasis on, or at least giving more recognition to, environmental factors that influence horn growth is logical, most of which are mediated through maternal nutrition and early life conditions (Festa-Bianchet and Jorgenson 1998, Monteith et al. 2009, Willisich et al. 2015) or through differences in the availability of resources needed to support growth (Bunnell 1978, Büntgen et al. 2014, Carvalho et al. 2017). Enhancing nutrition within populations has the potential to greatly improve growth in condition-dependent structures such as horns, but improving nutrition without shifting our focus away from males, horns, and genetics is unlikely to be successful. With all the hyperbole surrounding trophy management and big horns, we suggest the importance of females in the management of mountain sheep has been largely forgotten. Females play a critically important role, not just as the reproductive segment of the population responsible for producing young, but also in the size and growth of males, and their own abundance, in turn, affects population productivity through density-dependent feedbacks.

## Where Do We Go From Here?

When nutritional limitation causes declines in the size of secondary sexual traits (e.g., horn size), nutrient availability per individual can be enhanced in 2 primary ways:

enhancement of habitat or harvest of females, either of which can back the population away from nutritional carrying capacity (Monteith et al. 2014). The aim of habitat treatments is to increase nutritional carrying capacity, although the effectiveness of such treatments is limited by spatial scale, fiscal constraints, jurisdictional restrictions, and perceived risk by humans. In addition, the effects of those manipulations on nutritional condition can be short lived as the population grows and responds in a density-dependent manner. As an alternative, female harvest aims to lower density and regulate the population with respect to nutritional carrying capacity but is not subject to many of the same limitations as habitat manipulations.

*Habitat improvement.*—Methods available to enhance habitat quality by modifying vegetation and increase nutritional carrying capacity for mountain sheep include, among others, prescribed fire, mechanical or manual treatments, and chemical treatments (Bleich and Holl 1982, Holl et al. 2012). Singly, or in combination, application of those methods can set back vegetation succession and foster growth of more abundant and more palatable forage for large herbivores. Evidence pertaining to the net nutritional and fitness benefits for big game following habitat treatments, however, is limited (Bergman et al. 2014). Nevertheless, areas in topographically diverse country with large areas of high visibility and abundant, high-quality forage near escape terrain are typically considered prime habitat for mountain sheep (Geist 1971, Risenhoover and Bailey 1985, Bleich et al. 1997, Schroeder et al. 2010).

After decades of fire suppression and the ensuing effects on populations of mountain sheep, fire has been acknowledged as one of the most effective tools to create more and better forage for those ungulates (Riggs and Peek 1980, Hobbs and Spowart 1984, Etchberger et al. 1989, Holl and Bleich 2010, Greene et al. 2012). Although well recognized for its benefits, implementing prescribed fire or other habitat manipulations on mountain sheep ranges can be challenging, if not impossible (Bleich 2005). Further, implementing habitat treatments at a spatial scale likely to promote population-level benefits can be cost prohibitive (Beck et al. 2012). Moreover, fire may not be as costly as most habitat treatments, but it presents an element of danger and may not be socially or politically acceptable in some areas (Quinn-Davidson and Varner 2012). Indeed, wildfires continue to be suppressed in much of mountain sheep habitat including wilderness areas, and let-burn policies need to be considered.

Although well intended, legislation associated with wilderness designation in the United States can, and has, thwarted efforts to manage habitat to the benefit mountain sheep, including much needed natural or prescribed fire (Parsons 2000; Bleich 2005, 2016). When habitat manipulation is possible, it can be an effective tool to enhance nutrition and, thereby, positively influence horn growth. Nevertheless, the positive influence will be temporary because density-dependent responses in population productivity should propel the population towards nutritional carrying capacity until resource limitation once again suppresses growth of condition-dependent structures, either

as a result of population growth or through vegetative succession, both of which reduce the availability of nutrients to individual animals (Bowyer et al. 2014). When food resources are abundant (i.e., population well below nutritional carrying capacity), populations have the potential to grow rapidly in size until density-dependent feedback heightens, competition for resources increases, nutritional condition declines, and productivity and population growth subsides (Forsyth and Caley 2006, Monteith et al. 2014). Indeed, following cessation in female harvest at Ram Mountain, Alberta, Canada, density-dependent reductions in horn size of males coincided with an increase in mortality of young (Bérubé et al. 1996), a decline in mass of yearlings (Festa-Bianchet et al. 1995), and a delay in primiparity among females (Jorgenson et al. 1993a).

*Female harvest.*—We contend that extrinsic regulation (i.e., harvest of females) of populations of large herbivores is the most effective way to manage the degree of density dependence and, thus, nutritional limitation on growth of males. Translocation efforts have been an effective management tool for establishment and supplementation of some populations (Bleich et al. 1990, Krausman 2000, Hurley et al. 2015), and concomitantly may be a tool to reduce population abundance and, presumably, density-dependent effects within source populations. Nevertheless, translocations are expensive (Bleich 1990), politically challenging (Bleich 2005, 2016), not always successful (Singer et al. 2000), and difficult because locations offering viable habitat without livestock-related conflicts are increasingly rare (Singer et al. 2000, Shannon et al. 2014). Although effective in aiding conservation efforts in reestablishment of bighorn sheep throughout their range (Hurley et al. 2015), translocation is unlikely to be a long-term solution to regulating density of sheep populations (Rominger and Goldstein 2006). Furthermore, much like habitat enhancement efforts, translocations may be inhibited by wilderness legislation (Bleich 2005), whereas female harvest remains a viable management option. Hunting is actually one of the most accepted and cherished activities in designated wilderness (Semcer and Pozewitz 2013) and, therefore, presents a valuable opportunity to manage populations in lieu of the challenges to habitat management in such areas.

Wildlife management agencies across North America often restrict harvest of artiodactyls to males, especially for trophy species such as wild sheep (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008b). Of 20 state, provincial, or territorial jurisdictions managing mountain sheep in Canada and the United States,  $\leq 7$  allow harvest of females and all do so very conservatively (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008a). Among polygynous ungulates, few males are necessary to inseminate numerous females (Berger and Gompper 1999, Whitten 2001, Freeman et al. 2014). Thus, a male-biased or male-exclusive harvest strategy is considered conservative, because it protects the primary reproductive component of the population (McCullough 1979, Mysterud et al. 2002). Indeed, harvest restricted to males, and a conservative harvest of few, large males has a negligible effect

on demography of polygynous ungulates (McCullough 1979, 2001; Clutton-Brock et al. 2002; Mysterud et al. 2002) and, with the exception of exceedingly high harvest rates (Milner-Gulland et al. 2003), does almost nothing to limit population size (McCullough 1979). Unless exposed to heavy mortality from predation or disease (Cassirer et al. 2013, Johnson et al. 2013, Shannon et al. 2014), male-only harvest results in populations that are inherently regulated by their habitat and that, by consequence, are experiencing varying levels of nutritional limitation.

Female harvest as a management strategy remains unacceptable to many individuals, despite populations continuing to thrive and remain robust with some substantive female harvests in, for example, bison (*Bison bison*; Koons et al. 2015), North American elk (Walker 2011, Proffitt et al. 2013), white-tailed deer (Miller and Marchinton 1995, Walker 2011, Harper et al. 2012), pronghorn (O'Gara and Morrison 2004), and moose (*Alces alces*; Boertje et al. 2007) in North America, or red deer and moose in Europe (Solberg et al. 1999, Clutton-Brock et al. 2002, Milner et al. 2006, Rivrud et al. 2014). In contrast, harvest of female mountain sheep is rarely employed as a management tool (Wild Sheep Foundation Professional Biologist Meeting Attendees 2008a, Monteith et al. 2014), perhaps because of a reluctance of management agencies to face social animosity or unacceptance of such management by the public. Nonetheless, the idea that mountain sheep, large herbivores also regulated by density-dependent factors, would not respond to female harvest in a similar manner, or that their populations are somehow not subject to the same effects of resource limitation, is paradoxical. Like other large herbivores, mountain sheep are constrained by density-dependent processes, and harvest of females therefore, can be an effective tool to increase relative availability of nutrients by decreasing population density (Jorgenson et al. 1993b, Wishart 2006, Monteith et al. 2014).

In an experimental study at Ram Mountain, Alberta, Canada, an annual harvest of 12–24% of the female segment (ranging from 38 to 52 animals) of the population occurred for 9 years, followed by a 10-year cessation of female harvest that resulted in more than doubling the number of females in the population (Jorgenson et al. 1993b). Total population size remained relatively stable during the period when females were harvested, as did survival of males. An increase in the number of females after the experimental removal ended did not increase the availability of legal males or the number of males harvested (Jorgenson et al. 1993b). Males born when the population was regulated by female harvest grew larger horns by 4 or 5 years of age than males born thereafter (Jorgenson et al. 1993b) and, accordingly, the proportion of 6–7-year-old males that attained legal status (4/5 curl) declined from 66% to 34% following cessation of female harvest (Jorgenson et al. 1998). Indeed, as resource availability declined with increasing female density, females allocated fewer resources to growth of offspring (Festa-Bianchet and Jorgenson 1998), males allocated fewer resources to horn growth (Festa-Bianchet et al. 2004),

and males ultimately grew shorter and thinner horns (Jorgenson et al. 1998).

Following translocation to a new range, populations of large herbivores often exhibit irruptive dynamics in response to a wealth of forage resources in the previously unoccupied area (Forsyth and Caley 2006, Starns et al. 2014). Similar to enhancing nutrition by reducing density dependence through female harvest, male bighorn sheep harvested from a recently established population produced horns 10.6% larger at the same age as males harvested from the source population in New Mexico, USA (Rominger and Goldstein 2006). In addition to enhancing horn growth by reducing competition for limited resources and enhancing nutritional condition of remaining individuals, removal of females by harvest can increase population productivity and recruitment (Jorgenson et al. 1993b, Festa-Bianchet et al. 1998), increase production and yield of males (Jorgenson et al. 1993b, Clutton-Brock et al. 2002), promote stability of populations in variable environments, reduce susceptibility to disease, and bolster hunter opportunity.

*Density dependence and a variable environment.*—As nutritional condition improves with reduced population density, horn growth may increase, but improved condition also could manifest as a nutritional buffer against the vagaries of environmental variation. Many populations of mountain sheep reside in highly stochastic environments, whether they be subject to arid environments with extreme variation in forage production (Marshall et al. 2009, Creech et al. 2016), or more mesic environments subject to harsh winter weather (Mitchell et al. 2015). Effects of pulses of forage production or severe winters often are interpreted as density-independent; however, seldom are such situations independent of density (Bowyer et al. 2014). For example, following 3 years of intensive predator removal, density of a population of Dall's sheep in Alaska increased markedly (Mitchell et al. 2015). A subsequent severe winter resulted in a precipitous decline in that population, but an adjacent population where predators were not harvested exhibited no change in density following the severe winter (Mitchell et al. 2015). Similarly, recruitment of young in recently established populations of moose were less sensitive to the negative effects of warming climate and shifting plant phenology, likely because they were nutritionally buffered compared with populations that were established decades earlier (Monteith et al. 2015). Indeed, environmental stochasticity often affects populations already influenced by density dependence more so than those at lower density with respect to nutritional carrying capacity (Herfindal et al. 2006, Monteith et al. 2014).

Successful enhancement of habitat or implementation of a female harvest program to lessen the influences of density dependence and improve nutrition can be anticlimactic, both for the wildlife management practitioner and the ungulate population. Although immediate results often are expected and sometimes occur, lingering signatures of nutritional suppression can persist long after those pressures have been relieved. Recovery of vegetation following reductions in herbivory caused by high animal density can be slow, depending upon the vegetation types and the degree of

alteration (Fryxell et al. 1991, Olofsson 2006, Austrheim et al. 2008, Stewart et al. 2009, Speed et al. 2014). After vegetation has recovered or population densities have been effectively reduced, nutritional condition may well improve, but poor growth and small size of animals can persist for years because of intergenerational maternal effects (Mech et al. 1991, Freeman et al. 2013, Monteith et al. 2014). Multiple generations of animals following improved conditions may be required to overcome intergenerational effects of chronic nutritional stress (Monteith et al. 2009, Michel et al. 2016*b*).

*The nutrition–disease interface.*—The occurrence of epizootic pneumonia in bighorn sheep populations muddles the already complicated processes underlying population dynamics, and respiratory disease often is the cause of massive population crashes (Monello et al. 2001, Cassaigne et al. 2010, Cassirer et al. 2017). Respiratory disease has afflicted populations of bighorn sheep for the past century (Grinnell 1928) and, despite substantial research on the topic (Miller et al. 2012), pneumonia continues to be one of the most poorly understood diseases that afflict wildlife in North America (Plowright et al. 2013). Respiratory disease may be associated with multiple primary and secondary infectious agents, including *Mycoplasma ovipneumoniae*, *Mannheimia haemolytica*, *Pasteurella multocida*, and *Bibersteinia trehalosi* (Dassanayake et al. 2010; Besser et al. 2012, 2013). Having knowledge of the primary infectious agent is important, yet understanding the ecological and environmental conditions that prompt outbreaks and resulting widespread mortality are equally important (Cassirer et al. 2013, 2017).

Epizootic pneumonia outbreaks caused by bacterial respiratory pathogens are the underlying influence of massive mortality events, but frequency and intensity of die-offs are inconsistent and infections do not always manifest in disease (Miller et al. 1991, Cassirer et al. 2013, Shannon et al. 2014). Indeed, chronically infected animals sometimes continue to persist in affected populations (Plowright et al. 2013). Based on an extensive analysis of epizootics caused by respiratory disease from 99 herds across the range of bighorn sheep, 88% of pneumonia-induced die-offs occurred at, or within 3 years of, peaks in population size (Monello et al. 2001). As the influences of density dependence increase with growth of populations, declines in relative availability of food lead to reductions in nutritional condition.

Research across numerous taxa has connected processes of immune function with nutritional condition, food availability, and physiological stress (Stahlschmidt et al. 2015, van Dijk et al. 2015, Peck et al. 2016). For example, immune function was altered in North American elk and red deer as a function of suppressed nutritional condition in response to high density or manipulation of food availability (Landete-Castillejos et al. 2002, Downs et al. 2015). Indeed, immune function plays an important, but often underappreciated, role in fitness and performance of populations (Lochmiller 1996, Graham et al. 2010, Downs and Stewart 2014, Nussey et al. 2014). We suspect the potential interplay among density, nutrition, and immune function may hold fruitful avenues for research and, from a conservation perspective, management of mountain sheep populations in the presence of infectious

agents associated with respiratory disease. Although the hypothesis warrants testing, regulating densities by way of female harvest may aid in providing a density-dependent buffer against epizootic die-offs within populations through the nutritional benefits that are accrued as a result of that management action.

*Detecting resource limitation.*—In populations regulated by predation or recently experienced die-offs associated with disease (Cassirer et al. 2013, Johnson et al. 2013), habitat enhancement projects and harvest of females are unlikely to yield a strong positive effect on horn development (Jorgenson et al. 1998); those populations are likely well below nutritional carrying capacity and consequently, are not experiencing strong nutritional limitation. Similarly, in environments where intrinsic habitat quality is low, such as areas with large amounts of maintenance forage, recruitment of young may be low and adults persist at a poor nutritional plane with no apparent influence of density (Shea et al. 1992, Owen-Smith 2002, DeYoung 2011). Efforts to reduce population density or otherwise enhance resource availability are unlikely to be successful in achieving desired demographic or morphological changes when factors other than nutritional limitation regulate populations (Festa-Bianchet et al. 2006*a*, Johnson et al. 2013, Bowyer et al. 2014). Therefore, making informed management decisions is contingent upon understanding basic elements of population regulation and strategically collecting appropriate information to lend to that understanding.

Horn size and age data are collected routinely from harvested mountain sheep, in part because maintaining trophy quality is often an underlying management goal. Nevertheless, trends in horn data are likely poor criteria upon which to establish degree of nutritional limitation in populations because changes in horn size evident in the harvest are a product of age, nutrition, genetic factors, and biases associated with harvest data (Pelletier et al. 2012, Festa-Bianchet et al. 2015, Pigeon et al. 2016). Increasing or maintaining horn size may be a management objective, but measuring the mechanisms of change, as opposed to the response to management, will yield a more meaningful interpretation. Large herbivores undergo a suite of changes in life-history characteristics in response to density as changes in nutritional condition occur (Eberhardt 2002). The collective evidence of changes in population characteristics can provide valuable information about population regulation and where a population resides with respect to nutritional carrying capacity (Bowyer et al. 2005, 2013).

Changes in life-history characteristics, including growth and development, are ultimately a product of nutritional condition, which is a mechanistic link between factors that influence resource limitation and demographic processes (Monteith et al. 2014). Nutritional condition is an integrated measure of energetic debts and gains from the previous season (Parker et al. 2009, Monteith et al. 2013*b*); hence, quality and quantity of forage and its per capita availability are inherent within that metric (Monteith et al. 2014). As a result, nutritional condition, a product of an animal's environment (Franzmann 1985), can be used to indicate

the resource potential to sustain population growth, and thereby signifies the proximity of a population to nutritional carrying capacity (Monteith et al. 2014). Nutritional condition represents a useful ecological indicator for understanding population dynamics of large herbivores (Stephenson et al. 2002, Cook et al. 2010, Monteith et al. 2014) but also yields a direct assessment of the current nutritional state of the population, which can be used to assess the merit of habitat enhancement or female harvest programs (Monteith et al. 2014).

## MANAGEMENT IMPLICATIONS

Herein, we call for a renewed appreciation for the role of females in affecting size and yield of large males, both because of their effect on nutritional limitation within populations (i.e., density-dependent feedbacks) and, in turn, the potentially life-long influence of maternal condition on growth of young. We suggest that harvest of females is likely to be the most effective tool to modulate nutrition and, thereby, regulate the proximity of a population to nutritional carrying capacity. We acknowledge and fully appreciate that initiating female harvest may conflict with hunting and management traditions for mountain sheep and some other large ungulates; thus, shifting motivations of harvest may only be possible through increased public outreach and education.

We suspect that the prevailing resistance to female harvest stems from attitudes developed during the era of protection after the near extirpation of most large mammals at the turn of the twentieth century (Leopold 1933); however, robust populations of large mammals now occur throughout much of North America (Krausman and Bleich 2013, Hurley et al. 2015). Moreover, although harvest of only males is conservative and was necessary for the recovery of extirpated populations, an exclusively male harvest, in combination with the desire for large horns or antlers and the discovery of unintended consequences of harvest, has produced a nearly myopic focus on the genetic underpinnings of those traits. This dogma has diverted attention away from the ever-present and pervasive role of nutrition and, ultimately, the role of females in the growth and production of large males.

If production of large, trophy males remains an important management objective, a likely outcome in a hornographic culture, then we contend that management programs should integrate monitoring of the nutritional status of populations, seek to enhance nutrition where evidence indicates that resource limitation is occurring, and implement female harvest to enhance per capita nutrition in populations regulated by density-dependent processes. Ultimately, we call for greater recognition of the pervasive role of females in the production of trophy males, and that accordingly, females be better integrated into harvest and management programs.

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