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S. M. Barber-Meyer

University of Minnesota, shannonbarbermeyer@gmail.com

L. D. Mech

U.S. Geological Survey, Northern Prairie Wildlife Research Center

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REVIEW

FACTORS INFLUENCING PREDATION ON JUVENILE UNGULATES AND NATURAL SELECTION IMPLICATIONS

S.M. Barber-Meyer^{1,*} & L.D. Mech²

¹ Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Ave., Saint Paul, MN 55108, USA.

² U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 – 37th St. SE, Jamestown, ND 58401-7317, USA.

mailing address: The Raptor Center, 1920 Fitch Ave., University of Minnesota, St. Paul, MN 55108.

phone: 651-649-5231; fax: 651-649-5233; email: mechx002@umn.edu

* Corresponding author: Tiger Conservation Program Officer, World Wildlife Fund, 1250 24th St. NW, Washington, DC 20037 USA.

phone: 202-861-8265; email: shannonbarbermeyer@gmail.com

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Abstract

Juvenile ungulates are generally more vulnerable to predation than are adult ungulates other than senescent individuals, not only because of their relative youth, fragility, and inexperience, but also because of congenital factors. Linnell et al.'s (Wildl. Biol. 1: 209-223) extensive review of predation on juvenile ungulates concluded that research was needed to determine the predisposition of these juveniles to predation. Since then, various characteristics that potentially predispose juvenile ungulates have emerged including blood characteristics, morphometric and other condition factors, and other factors such as birth period, the mother's experience, and spatial and habitat aspects. To the extent that any of the physical or behavioral traits possessed by juvenile ungulates have a genetic or heritable and partly independent epigenetic component that predisposes them to predation, predators may play an important role in their natural selection. We review the possible influence of these characteristics on predisposing juvenile ungulates to predation and discuss natural selection implications and potential selection mechanisms. Although juvenile ungulates as a class are likely more vulnerable to predation than all but senescent adults, our review presents studies indicating that juveniles with certain tendencies or traits are killed more often than others. This finding suggests that successful predation on juveniles is more selective than is often assumed. Because we are unable to control for (or in some cases even measure) the myriad of other possible vulnerabilities such as differences in sensory abilities, intelligence, hiding abilities, tendency to travel, etc., finding selective predation based on the relatively few differences we can measure is noteworthy and points to the significant role that predation on juveniles has in the natural selection of ungulates. Future research should compare characteristics, especially those known to influence survival, between animals killed by predators versus those killed by other sources as well as survivors versus non-survivors to better understand predation's role in natural selection.

Introduction

Predation is an important agent in evolution [1-3]. For predation to impact the natural selection of ungulates, the probability of individual ungulates being killed by predators must vary, and survivors must reproduce [4]. Predation's effect on ungulate genetic transmission is greatest on pre-breeders because this cohort has not yet transmitted any genes. Predation on pre-breeders including neonates, young-of-the-year, and other juveniles, may have a high impact on ungulate population dynamics because variable juvenile survival (coupled with the high and stable adult survival seen in most ungulate populations, [4]) could greatly influence population fluctuations

[5-9]. Although equivalent variation in adult survival would have a greater impact on ungulate population dynamics [8,10], variation in juvenile survival may have a greater realized impact [9] because adult survival routinely exhibits little variability (likely a canalized trait against temporal variation) [11]. Predators select juveniles and very old animals disproportionately [12-23]. However, predation's effect in natural selection is not equal across all species of juvenile ungulates but depends in part on length of vulnerability [24-27], for example whether neonates are followers or hidiers (see Selection mechanisms).

Neither is predation's effect necessarily equal across all juvenile ungulates of a single species, for predation's precise effect may depend on the differing hunting techniques of various predators [28,29]. For example, coursers such as wolves (*Canis* spp.) and hyaenas (*Crocuta crocuta*) elicit a flight response followed by sorting of the herd [30], and coursing generally leads to the capture of prey in poorer condition [12,22,29,31]. This relationship may be important in the natural selection for generally healthy and strong juvenile ungulates [17]. In contrast, large cats such as cougars (*Puma concolor*) usually kill by stalking and surprise attack where the condition of the prey might not always be a strong predictor of capture [32-34]. However, stalking predators may be important in the natural selection of the mothers' and neonates' movements, hiding ability [17], alertness, and awareness of their surroundings (here we define neonates as individuals from birth to 1-week of age). Intermediate predators (between coursers and stalkers) such as coyotes (*C. latrans*) may influence selective pressure on the general health and strength and the hiding ability and awareness of neonates.

Within ungulate species, predation effects also vary greatly over the range of densities or predator/prey ratios at which they exist. Caribou, for example, range from barren-ground populations where hundreds of thousands of offspring are produced in aggregations and predator/caribou ratios are very low [35], to mountain caribou or woodland caribou that occur at relatively low densities with other ungulate prey and therefore higher predator/caribou ratios [36,37].

A variety of studies (see [38] for review) has shown predation to be an important mortality source for juvenile ungulates (including moose, *Alces alces*; caribou, *Rangifer tarandus*; bison, *Bison bison*; elk, *Cervus elaphus*; white-tailed deer, *Odocoileus virginianus*; pronghorn, *Antilocapra americana*; and Thomson's gazelle, *Gazella thomsoni*) and demonstrates that some carnivores are particularly effective predators on juveniles (including wolf, *C. lupus*; grizzly bear, *Ursus arctos*; black bear, *U. americanus*; cougar; bobcat, *Lynx rufus*; cheetah, *Acinonyx jubatus*; and African wild dog, *Lycaon pictus*) [1,39-47].

Here we review research on characteristics that potentially predispose individuals to predation within the vulnerable juvenile age class. These studies show either different characteristics between the predator-killed juveniles versus those not killed by predators or varying characteristics between survivors and non-survivors where predation was either the leading or a major cause of death. While the 1st type of study clearly depicts predation's potential impact on natural selection, the 2nd type of study may merely show that predators are selecting the same characteristics that otherwise predispose juveniles to mortality in general and thus, superficially appear to indicate little impact on natural selection. However, the 2nd type of study is still important to our review because even if predation and other causes of mortality (e.g., starvation) are acting on the same traits, the selection pressure from predation is

likely to be greater and thus, animals in mid-condition are less likely to survive than in the absence of predation. Linnell et al.'s [38] review found neonatal mortality (from all causes) averaged $47\% \pm 24$ ($N = 68$) in areas with predators but only averaged $19\% \pm 8$ ($N = 6$) in predator-free areas. This difference suggests that even if the factors influencing mortality were the same with or without predators, selection acting on those factors would likely be stronger in the presence of predation.

Characteristics that might predispose juveniles to predation could be primary causes of that predisposition or they may merely be associated with the true cause. These characteristics could be environmentally based, genetic, or both. Studies of red deer (*Cervus elaphus*) demonstrate that juvenile survival has a genetic basis [48,49] and suggest that “associations between fitness and genotype are common” [49: 434]. Also, recent epigenetic (“heritable changes in gene expression and function that cannot be explained by changes in DNA sequence” [50: 106]) research indicates that in some cases environmentally-induced natural variation can be inherited at least partly independent of genetic variation [50] and that this variation can affect behavior [51]. Specific links between genotype, genetic expression, and vulnerable phenotypes are not yet known for many characteristics that influence juvenile survival, because these associations are studied so little in wild populations [49,50]. Therefore we are unable to estimate the effect size of epigenetic and genetic heritability on juvenile mortality. However, we review as many of these characteristics as possible, with the assumption that there are likely genetic (and possibly epigenetic [50]) components to at least some of them [49] that may be important to selection.

Blood characteristics

Blood characteristics (especially long-term seasonal trends among collective characteristics) can reflect an animal's internal condition [52,53]. Therefore, mortality studies where blood is sampled upon capture can help determine whether the condition deficiencies indicated by blood characteristics influence the individual's susceptibility to predation. While blood characteristics can signify individual condition differences, they may also reflect differences in age, sex, season, reproductive status, recent feedings, capture methods, and the processing of samples [54-59]. Thus, emphasis should be placed on similar (or ideally, standardized) methods in research done for comparisons among studies. As metabolic pathways are better understood, interpretation of blood profiles will improve.

Currently, no single blood characteristic is known to consistently and accurately predict general ungulate condition [52,57,58,60-64]. In fact, in isolation, both high and low values of some blood characteristics can be associated with either diseased or healthy animals (e.g., serum urea nitrogen, white blood cells counts, creatinine, gamma globulins; [52,53]). Despite these limitations, emerging research shows that blood characteristics are useful in determining predisposition to mortality.

Hematology

Changes in white blood cell count (WBC) are associated with a variety of infections [52], and mean WBC was lower in white-tailed deer neonates in Minnesota that died ≤ 1 week of birth compared to survivors [65].

Sams et al. [66] found that lower mean corpuscular hemoglobin concentration (MCHC), an erythrocyte index, was sometimes associated with low-protein diets in captive white-tailed deer fawns. MCHC was lower in Minnesota white-tailed deer neonates that died ≤ 1 week of birth compared to survivors [65].

Mean hemoglobin concentration, packed cell volume, and mean corpuscular volume (MCV) were lower in Minnesota white-tailed deer neonates that died at 2-4 weeks old [65]. Captive white-tailed deer does fed a low-protein diet had fawns with lower MCV, an erythrocyte index [66]. Severely starved mule-deer fawns had decreased hemoglobin and erythrocytes [67].

Total protein and gamma globulins

Hypoproteinemia can be associated with trauma (including wounds or burns) or renal disease [52]. Depressed blood protein may reflect a poor diet [52,57]. Wyoming elk calves that survived through approximately 2 months (Jul 31) had higher total protein [68].

Serum gamma globulin (GG) is associated with antibodies, and in young animals lower levels may reflect their developing immune systems [57] or delayed development of the neonate's gut function due to nutritionally restricted mothers [69]. Depressed GG has also been associated with increased septicemia, diarrhea, and neonatal mortality in captive ungulates [70-74]. GG was lower in mortalities of white-tailed deer neonates < 21-days old than in survivors and was important in predicting mortality to 21 days where predation and emaciation were major sources of mortality [75]. Higher levels of GG in northern Yellowstone elk neonates were associated with increased summer survival, and predation was the major mortality source [47].

Glucose

Juvenile ungulates experiencing hypoglycemia may be under extreme starvation or other digestive/nutritional disorders [52,76]. Elevated glucose levels in elk calves were associated with well-fed, rapidly growing calves as compared to their smaller, nutritionally restricted counterparts [77]. Sams et al. [66] found that lower blood glucose was sometimes associated with captive white-tailed deer fawns born to does fed a low-protein diet. Glucose was higher in Wyoming elk calves surviving through approximately 2 months (31 Jul) where predation was the major mortality source [68]. While glucose levels can be artificially elevated during capture [59], evaluating relative differences among juveniles within a study, rather than absolute values compared across studies, may still indicate relative condition.

Plasma enzymes

Alkaline phosphatase (AP) is a hormone concentrated in osteoblasts associated with growth (e.g., pregnancy, antler development, and juvenile growth) [76]. Calves with elevated AP are likely in a growth phase, whereas depressed AP indicates possible malnutrition [52,77]. In general, larger elk calves have higher AP at birth [77] and food-restricted red deer have lower AP [78]. Wild pronghorn fawns in better nutritional condition had higher AP [63]. Elk consuming better diets in areas following a burn

also had higher AP than elk without access to burned areas [78]. AP was higher in Wyoming elk calves that survived to approximately 2 months (Jul 31) [68].

Serum gamma glutamyltransferase (GGT) concentration is an index of colostral absorption efficiency [79,80], and depressed levels may indicate inability to nurse [81]. GGT was lower in Oklahoma white-tailed deer neonate mortalities than survivors < 21-days old and was an important predictor of mortality to 21-days old [75].

Lactic dehydrogenase (LDH) is an enzyme important in lactic acid – pyruvic acid conversion and is found in many tissues. Elevated LDH is associated with tissue breakdown and stress and excitability during capture [57]. In captive white-tailed deer fawns, elevated LDH was associated with dams fed a low-protein diet [66]. In humans, elevated LDH may indicate multiple disorders including problems with lungs, heart, and liver tissues [52]. LDH was lower in Wyoming elk calves that survived to approximately 2 months from birth (31 Jul) [68].

Serum urea nitrogen

Serum urea nitrogen (SUN) is an indicator of protein quality in the diet and has been related to nutritional condition in white-tailed deer [82,83]. Isolated interpretation of SUN is difficult as moderately high levels may indicate increasing levels of dietary protein intake [76], while high-energy diets may cause low SUN due to the rumen microbes more efficiently using the proteins, thus producing less urea [84]. SUN was higher in white-tailed deer fawns with higher survivability in one study [43], but tended to be lower in those that survived to 1 week in another [65] as well as in elk calves that survived to approximately 2 months (31 Jul) [68]. SUN was also higher in food-restricted red deer than in deer fed a control diet [78]. Extremely high SUN in non-survivors may indicate catabolism of body proteins if nursing bouts are inadequate [62,65,78,82,83], or it may indicate renal failure [52,78].

NEFA and triglycerides

Depressed non-esterified fatty acids (NEFAs) may indicate marginal fat reserves [85] and a poor diet [67]. NEFAs were lower in Minnesota adult and fawn white-tailed deer killed by wolves in late winter as compared to deer not killed by wolves [58].

Triglycerides, a measure of fat metabolism, can be an indicator of pathology in humans when too high or low, but little is known about the influence of different levels on wildlife. Triglycerides tended to be lower in white-tailed deer neonates in Minnesota surviving through week 1 [65]. In contrast, serum triglycerides were elevated in a pronghorn herd in better long-term nutritional condition than in 2 other herds [63].

Electrolytes

Mean phosphorus concentration was higher in Wyoming elk calves that survived to approximately 2 months (31 Jul) [68]. Calves with reduced phosphorus may be suffering from dietary deficiencies as the lack of phosphorus is often associated with a simple lack of intake [52].

Mean potassium concentration was lower in Minnesota white-tailed deer neonates that died at ≤ 1 week and when 2-4 weeks old [65]. Decreased serum potassium may indicate inadequate nursing and lower nutritional condition [83]. In contrast, Sams et al. [66] found that higher potassium concentrations were sometimes associated with captive white-tailed deer fawns born to does fed a low-protein diet.

Decreased calcium has been associated with starvation [52], and higher calcium with improved condition in adult moose [57]. Mean calcium concentration was lower in Minnesota white-tailed deer fawns that died when 5-12 weeks old [65]. In contrast, Sams et al. [66] found higher calcium concentrations were sometimes associated with captive white-tailed deer fawns born to does fed a low-protein diet.

Cortisol

Increased cortisol may indicate increased catabolism due to restricted nutrition or capture-induced stress [56,83,86-88]. Cortisol was higher in nonsurviving white-tailed deer neonates in Minnesota than in survivors 5-12 weeks old [65].

Tumor necrosis factor- α

Tumor necrosis factor- α (TNF- α) is a cytokine secreted by T-cells [89] that functions as a major mediator in host immune responses including the production of interleukin-6 [90], lysis of virally infected cells, and antitumor activity [91]. Elevated TNF- α likely indicates the animal is stressed and undergoing an immune response [92], and long exposure to elevated levels has been associated with body wasting [92]. Neonatal white-tailed deer that died tended to have higher immunoreactive TNF- α levels than did survivors < 21 -days old [92]. Similarly, in Minnesota white-tailed deer fawn non-survivors through 1 week and between 2-4 weeks old tended to have higher TNF- α levels [65]. In contrast, TNF- α levels were not important predictors of survival in northern Yellowstone elk calves through their first 20 weeks [47].

Morphometric and other condition factors

Birth weight

In many studies where predation was the major cause of death among juveniles, increased survival has been correlated with heavier birth weight. This may be because birth weight reflects condition [93] and because light-born neonates often have difficulty nursing, which confounds their nutritional depression [94]. In west central Montana, heavier neonate elk calves also had increased survival [9]. In Yellowstone National Park, predators killed more light-born elk calves during 1987-1990 [95], although this was not the case in elk neonates during 2003-2005 [47]. Estimated birth weight was higher in Minnesota white-tailed deer neonate survivors [43] and in those that survived when ≤ 1 -week old and during weeks 5-12 than in those that died [65]. Similarly, the majority of white-tailed deer fawns in an Illinois study killed by canids were light to average in mass near birth [96]. In moose calves, time to death was significantly related to birth weight [97], and in caribou, calves with greater birth weight had higher summer survival [36].

Size

Skeletal development (e.g., girth, hind-leg length) of Minnesota white-tailed deer was less in neonates that died within 1 week than in survivors [65]. Skeletal development along with birth weight likely reflects neonatal robustness [93].

Marrow fat content

Marrow-fat content can be used as a 1-way test to indicate the extent to which an animal has used fat reserves. Because marrow fat is 1 of the last fat stores to be accessed, an animal with low marrow fat has depleted most other fat reserves and is likely in poor condition [98]. Wolf-killed, 6-10-month old, white-tailed deer fawns had significantly lower femur-marrow fat than those killed by accidents in the same area [99,100]. Interpretation of marrow-fat content in very young animals remains difficult because the rate of marrow deposition is not well studied [101].

Maternal and grandmaternal condition

Wolves killed more caribou calves in Denali National Park after winters of deep snow when these calves were still *in utero* and presumably their mothers were in poorer nutritional condition than after winters with average snow depth [31]. Moose calves in 2 areas of Alaska, where predation was a major mortality source, born to mothers in poor condition the previous autumn had higher mortality than those from mothers in good condition [97,102]. In Minnesota, where predation on juvenile white-tailed deer is a major source of mortality [43], survival of deer to 2 years was positively influenced by the grandmother's nutritional condition [103].

Other factors

Birth period

Whether a neonate is born during the pre-peak, peak, or post-peak period of the birthing season may have an important influence on survival [24,27,104,105]. Pre-peak neonates survive better if born before predators congregate on birthing grounds or before predators sharpen their search image. Early-born neonates also may have longer access to high-quality forage (e.g., bighorn sheep, *Ovis canadensis*, [106], and mountain goats, *Oreamnos americanus*, [107]). Increased forage access may allow young ungulates to attain superior condition before the nutritionally restrictive winter and may give them an advantage in escaping predators [106,108-110]. For example, early-born moose calves in southcentral Alaska, where bear predation was a major source of juvenile mortality, had higher survival than those born later [44]. Roe deer (*Capreolus capreolus*) neonates born during the peak were more likely to die from predation [111].

Alternatively, neonates may benefit from being born during the peak of birthing due to the dilution effect [112-114], the confusion effect [115], and/or the increased defense afforded by numerous vigilant mothers [24,104,116-118]. For example, early wildebeest (*Connochaetes taurinus*) studies in Tanzania concluded that birth

synchrony in time and space effectively swamped predators, resulting in predators killing fewer calves during peak birthing [24]. Caribou in Denali National Park, born within 2-3 days of the median birth date had 50% better survival following low-snowfall winters than calves born earlier or later [37]. Similarly, Mentasta-herd caribou in Alaska had higher survival if born during peak birthing [36].

Conversely, late-born calves have been associated with mothers in poorer condition [119,120], predisposing them to greater mortality. In Alaskan moose calves, time to death decreased as birth date increased [97], and late-born Alaskan caribou calves had lower survival than peak or early-born calves [35]. In Yellowstone National Park, predators killed more late-born elk calves during 1987-1990 [95], and during 2003-2005, peak-born calves had the highest summer survival [47]. Also, early-born elk calves had lower survival in west-central Montana [9]. Conclusions about the importance of birth period in mortality studies may differ depending on whether births are classed into 2 categories (e.g., early and late) or into 3 categories (e.g., early, peak, and late) and whether the study measures only the core birthing period (i.e., 80% of births) or a longer period.

Mother's experience

The learning ability and experience of a mother is likely an important selection factor in terms of her ability to hide and move her offspring, her defensive tactics, her detection of predator abundance, knowledge of escape routes, and access to food resources [108,121-124]. Semi-captive, white-tailed deer dams \geq 4-yr old in Michigan lost proportionally only slightly more neonates when bears were present vs. absent, whereas younger dams lost significantly more when bears were present [122]. Fawn: doe ratios during Dec and Apr in Minnesota white-tailed deer subject to wolf and black bear predation were positively related to maternal age [123]. Similarly, in another Minnesota study where black bear and wolf predation equally accounted for all fawn mortalities fawns from mothers $>$ 4-yr old weighed more and survived better [43].

Spatial and habitat aspects

Other prey attributes including preferences for herd versus dispersed grouping behavior, open versus closed habitats, etc. may also influence predation effects. Caribou from both the Mentasta and Denali herds in Alaska survived better when born in core calving areas rather than in peripheral areas [36,37]. Mentasta-herd caribou juveniles born in areas of mottled snow survived longer than those born in sedge-tundra habitat [36]. Roe deer fawns that used woodland suffered less predation than those that used pasture [111]. In Porcupine-herd caribou calves, survival was higher at lower elevations, and predation tended to be greater in higher areas [35]. In Yellowstone National Park, elk calves born near a residential area (Mammoth Hot Springs) survived much longer than calves born elsewhere along Yellowstone's northern range, likely due to reduced predator densities near residential areas [47]. Similarly, higher elk calf: cow ratios were documented near roadsides in Jasper National Park, Canada, in contrast to areas near wolf dens [125].

Implications

Predation may select for physical or behavioral traits of juvenile ungulates that have a genetic component (and possibly a heritable and partly independent epigenetic component [50]) and so may be important in natural selection. The amount of phenotypic variation in a trait explained by genetic factors (e.g., additive genetic variance) exclusive of the influence of environmental factors has been defined as the trait's genetic heritability [126]. While it is the heritability of animals' physical traits that are best documented (e.g., collared flycatcher, *Ficedula albicollis*, tarsus, wing, tail, and beak lengths [127]; bighorn ram, *O. canadensis*, body weight and horn size [128]; average heritability of skeletal metric traits in Rhesus macaques, *Macaca mulatta* [129]; human body weight and height [130]), heritabilities of some behavioral and mental traits have also been documented (e.g., exploratory behavior in mice, *Mus* [131]; flight time in crossbred tropical beef cattle, *Bos indicus* x *Bos taurus* [132,133]; human personality [134]; human IQ [130]). Furthermore, other behavioral traits have a genetic component such as, in mice, maternal care [135], aggressive behavior [136], and anxiety [137]. Other traits including disease (e.g., human juvenile arthritis [138,139]) and juvenile survivability (e.g., red deer calf [48,49]) also have genetic components. Interestingly, mate choice behavior of mice was recently shown to have a heritable epigenetic component three generations removed from the treatment event [51]. To the extent that any of the physical or behavioral traits possessed by juvenile ungulates have a heritable component that predisposes them to predation, predators may play an important role in their natural selection. Even if these traits also predispose juvenile ungulates to increased mortality from non-predation sources, predation is still important in that it likely increases the selective pressure on these traits.

Selective predation on vulnerable juveniles may shape ungulates in many ways. Selective predation on juveniles in poor condition, as documented above by a variety of factors (e.g., collective blood characteristics, low marrow-fat content, low birth weight, reduced size), would generally lead to a juvenile cohort containing healthier, more-robust individuals. However, other factors might be selected for as well. For example, increased predation on juveniles whose grandmothers had been malnourished may select for strains with better ability to secure higher quality forage over the long term, resulting in ungulates able to extract more nutrients from limited resources (effectively increasing the carrying capacity of a given habitat). Although this principle was documented as a cohort effect [103], there is no evidence to suggest that the principle does not apply in general.

As for synchronized birthing, high predation may not necessarily result in more synchronized birthing [140], but high predation on juveniles born outside the peak birthing period should do so. However, if enough juveniles are born during the peak, a small number born outside the peak may survive on average equally well, provided there are few enough to be under the threshold of alerting predators and provided the neonates are not born outside of forage constraints (i.e., before spring green-up or too late to acquire fat reserves needed for winter). Nevertheless, early births to maximize summer weight gain and development, and late births attributed to young females and those in poor condition could offset predation's effect.

If there is selection for juvenile ungulates and their mothers to use certain kinds

of habitat this might lead to a general shift in landscape utilization. Ungulates could move into habitats of poorer forage to avoid high predator densities or into habitats with less cover where they might be less likely to be ambushed by stalking predators.

The implications of selective predation on juvenile ungulates that we have detailed above are limited by the lack of reported differences among juveniles, by the scarcity of what can be measured, and by the 1-way nature of the measurements (e.g., they can only show if an animal was not fit). For example, an animal with high marrow-fat killed by a predator may not have been close to starving, but it could possess other unmeasured vulnerabilities such as myopia (near-sightedness). Because we are unable to control for (or in some cases even measure) the myriad of other possible vulnerabilities such as differences in sensory abilities, intelligence, hiding abilities, tendency to travel, etc., finding selective predation based on the relatively few differences we can measure is noteworthy [12: 260] and points to the significant role that predation on juveniles has in the natural selection of ungulates.

Also, many of the factors that influence vulnerability (e.g., birth weight, sex) may be interactive with other factors or with the environment [49]. For example, a particular juvenile with low alkaline phosphatase (presumably poorer condition) in a predator-rich environment may be less vulnerable than a juvenile with normal alkaline phosphatase, depending on the relative ability of their respective mothers to hide them. While little research has been done on the links between genetics and fitness in wild populations because of numerous logistical difficulties, what has been done suggests the existence of such links may be common [49]. Continued research is also needed to determine the extent to which heritable epigenetics may influence an organism's "resistance to predators" [50: 111]. Indeed, even basic research is required to further epigenetic understanding such as determining "the rate of spontaneous epimutations in natural populations, let alone their stability over time" [50: 113].

Selection mechanisms

Infant ungulates can be categorized into followers and hidiers [141-143]. Follower neonates generally accompany their mothers just after birth while hidiers remain concealed for days to weeks after birth with few but long visits from their mother for feedings [144]. Superficially, selective predation on neonate followers (e.g., wildebeest, bison, caribou) appears relatively straightforward. Follower neonates in poor nutritional condition would presumably be easier to catch, all else being equal, when chased by predators than those in better condition, although some studies have not found this [37]. The mechanisms of selective predation on neonate hidiers (e.g., white-tailed and mule deer, red deer, elk) that are more vulnerable than others are not readily apparent because presumably all hidiers are vulnerable if detected by a predator at least for their first few days of life [145,146] until they are able to escape by running [147], or reach the age when they join their mother or the herd. As with followers, nutritional condition likely plays a role in selective predation, especially because hidiers able to grow quickly can better escape predators.

However, neonates may also be vulnerable to predation due to many types of factors other than nutritional condition. Such factors as the defensive, perceptive, physical, and behavioral traits and abilities of both the neonate and its mother could all play

a role in the security of the neonate from predation. Examples are many that remain currently immeasurable [1,13,145-198] and include the mother's ability to select a birthing site away from predators; and the mother's and neonate's abilities to detect predators, to gain information from the vigilance of the herd, and to learn from experience.

Conclusions

Although juvenile ungulates as a class are likely more vulnerable to predation than all but senescent adults, our review presents studies indicating that juveniles with certain tendencies or traits are killed more often than others. This finding suggests that successful predation on juveniles is more selective than is often assumed.

Regardless of the natural-selection mechanisms and our inability to measure many of the probable important predisposing factors to predation, predation on juveniles in poor condition would likely lead to overall better condition of the remaining cohort (and therefore, better condition, on average of their offspring as well). This effect is best documented in coursing predators (e.g., wolves, [12]; spotted hyenas, [29]). Predation by stalking predators (e.g., cougars, [32-34]) might not result in a similar increase in overall condition of the survivors due to differences in the mechanisms of prey selection but may result in other changes, such as prey habitat selection and other behaviors that may reduce exposure to ambush by stalking predators [199,200]. Therefore, the nature of the selective role of predation on juvenile ungulates will be different for each type of predator.

Finally, to better elucidate the ways in which natural selection may be occurring through predation on the more vulnerable individuals within the generally vulnerable juvenile age-class, it is important that juvenile-ungulate-mortality studies screen for factors that may influence vulnerability to predation, especially those known to influence survival. Importantly, future research should compare characteristics between animals killed by predators versus those killed by other sources as well as survivors versus non-survivors to better understand predation's role in natural selection.

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