# Factors Influencing Predation on Juvenile Ungulates and Natural Selection Implications

## S.M. Barber-Meyer[1],* & L.D. Mech[2]

[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

**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 hiders (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 barrenground 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% ± 24 (N = 68) in areas with predators but only averaged 19% ± 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**

Hypoprotenemia 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 ≥ 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 hiders [141-143]. Follower neonates generally accompany their mothers just after birth while hiders 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 hiders (e.g., white-tailed and mule deer, red deer, elk) that are more vulnerable than others are not readily apparent because presumably all hiders 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 hiders 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.

### References

1.  White, M., Knowlton, F.F. & Glazener, W.C. 1972. Effects of dam-newborn fawn behavior on capture and mortality. J. Wildl. Manage. 36: 897-906. doi:10.2307/3799446

2.  Vermeij, G.J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, Massachusetts, USA.

3.  Dawkins, R. & Krebs, J.R. 1979. Arms races between and within species. Proc. R. Soc. Lond., B 205: 489-511.

4.  Vermeij, G.J. 1982. Unsuccessful predation and evolution. Am. Nat. 120: 701-720.
    doi:10.1086/284025

5.  Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. 1998. Population dynamics of large herbivores:
    variable recruitment with constant adult survival. Trends Ecol. Evol. 13: 58-63.
    doi:10.1016/S0169-5347(97)01237-8

6.  Allee, W.C., Emerson, A.E., Park, O., Park, T. & Schmidt, K.P. 1949. Principles of animal ecology.
    Saunders, Philadelphia, Pennsylvania, USA.

7.  Pimlott, D.H. 1967. Wolf predation and ungulate populations. Am. Zool. 7: 267-278.

8.  Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000. Temporal variation in
    fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. 31: 367-393.
    doi:10.1146/annurev.ecolsys.31.1.367

9.  Raithel, J.D. 2005. Calf elk survival in west-central Montana and its impact on population dynamics.
    M.S. Thesis, University of Montana, Missoula, Montana, USA.

10. Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:
    2841-2854.

11. Gaillard, J.-M., & Yoccoz, N.G. 2003. Temporal variation in survival of mammals: a case of
    environmental canalization? Ecology 84: 3294-3306.
    doi:10.1890/02-0409

12. Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History
    Press, New York, USA.

13. Banfield, A.W.F. 1954. Preliminary investigation of the barren-ground caribou. Part I. Former and
    present distribution, migrations, and status. Can. Wildl. Serv., Wildl. Manage. Bull. 1 (10A): 1-79.

14. Fuller, W.A. 1966. The biology and management of bison of Wood Buffalo National Park. Can.
    Wildl. Serv., Wildl. Manage. Bull. 1 (16): 1-52.

15. Voigt, D.R., Kolenosky, G.B. & Pimlott, D.H. 1976. Changes in summer foods of wolves in central
    Ontario. J. Wildl. Manage. 40: 663-668.
    doi:10.2307/3800561

16. Carbyn, L.N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl.
    Manage. 47: 963-976.
    doi:10.2307/3808155

17. FitzGibbon, C.D. & Fanshawe, J.H. 1989. The condition and age of Thomson's gazelles killed by
    cheetahs and wild dogs. J. Zool., Lond. 218: 99-107.

18. Boyd, D.K., Ream, R.R., Pletscher, D.H. & Fairchild, M.W. 1994. Prey taken by colonizing wolves
    and hunters in the Glacier National Park area. J. Wildl. Manage. 58: 289-295.
    doi:10.2307/3809393

19. Carbyn, L.N., Lunn, N.J. & Timoney, K. 1998. Trends in the distribution and abundance of bison in
    Wood Buffalo National Park. Wildl. Soc. Bull. 26: 463-470.

20. Long, R.A., O'Connell Jr., A.F., & Harrison, D.J. 1998. Mortality and survival of white-tailed deer
    *Odocoileus virginianus* fawns on a north Atlantic coastal island. Wildl. Biol. 4: 237-247.

21. Ballard, W.B., Whitlaw, H.A., Young, S.J., Jenkins, R.A. & Forbes, G.J. 1999. Predation and survival
    of white-tailed deer fawns in northcentral New Brunswick. J. Wildl. Manage. 63: 574-579.
    doi:10.2307/3802645

22. Mech, L.D. & Peterson, R.O. 2003. Wolf-prey relations. In: Mech, L.D. & Boitani, L. (eds.). Wolves:
    behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA, pp. 131-157.

23. Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. 2004. Winter prey
    selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. J. Wildl. Manage.
    68: 153-166.
    doi:10.2193/0022-541X(2004)068[0153:WPSAEO]2.0.CO;2

24. Estes, R.D. 1976. The significance of breeding synchrony in the wildebeest. E. Afr. Wildl. J. 14: 135-152.

25. O'Donoghue, M. & Boutin, S. 1995. Does reproductive synchrony affect juvenile survival rates of northern mammals? Oikos 74: 115-121.
doi:10.2307/3545680

26. Twigg, L.E., Lowe, T.J., Martin, G.R., Wheeler, A.G., Gray, G.S., Griffin, S.L., O'Reilly, C.M., Butler, T.L., Robinson, D.J. & Hubach, P.H. 1998. The ecology of the European rabbit (*Oryctolagus cuniculus*) in coastal Western Australia. Wildl. Res. 25: 97-111.
doi:10.1071/WR97066

27. Testa, J.W. 2002. Does predation on neonates inherently select for earlier births? J. Mammal. 83: 699-706.
doi:10.1644/1545-1542(2002)083<0699:DPONIS>2.0.CO;2

28. Schaller, G.B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago, Illinois, USA.

29. Kruuk, H. 1972. The spotted hyena: a study of predation and social behavior. University of Chicago Press, Chicago, Illinois, USA.

30. Estes, R.D. & Goddard, J. 1967. Prey selection and hunting behavior of the African wild dog. J. Wildl. Manage. 31: 52-70.
doi:10.2307/3798360

31. Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., & Dale, B.W. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota, USA.

32. Hirst, S.M. 1965. Ecological aspects of big game predation. Fauna and Flora 16: 3-15.

33. Schaller, G.B. 1967. Hunting behavior of the cheetah in the Serengeti National Park. E. Afr. Wildl. J. 6: 95-100.

34. Hornocker, M.G. 1970. An analysis of cougar predation upon mule deer and elk in the Idaho primitive area. Wildl. Monogr. 21: 5-39.

35. Whitten, K.R., Garner, G.W., Mauer, F.J. & Harris, R.G. 1992. Productivity and early calf survival in the porcupine caribou herd. J. Wildl. Manage. 56: 201-212.
doi:10.2307/3808814

36. Jenkins, K.J. & Barten, N.L. 2005. Demography and decline of Mentasta caribou herd in Alaska. Can. J. Zool. 83: 1174-1188.
doi:10.1139/z05-111

37. Adams, L.G., Singer, F.G. & Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. J. Wildl. Manage. 59: 584-594.
doi:10.2307/3802467

38 Linnell, J.D.C., Aanes, R. & Andersen, R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildl. Biol. 1: 209-223.

39. Beale, D.M. & Smith, A.D. 1973. Mortality of pronghorn antelope fawns in western Utah. Proc. Bienn. Pronghorn Antelope Workshop 12: 41-52.

40. Schlegel, M. 1976. Factors affecting calf elk survival in northcentral Idaho. A progress report. In: Proceedings of the 56th Annual Conference of the Western Association of State Game and Fish Commissioners, Sun Valley, Idaho, USA, 26-29 July 1976, pp. 342-355.

41. Ballard, W.B., Whitman, J.S. & Reed, D.J. 1991. Population dynamics of moose in south-central Alaska. Wildl. Monogr. 114: 1-49.

42. Festa-Bianchet, M., Urquhart, M. & Smith, K. 1994. Mountain goat recruitment: kid production and survival to breeding age. Can. J. Zool. 72: 22-27.

43. Kunkel, K.E. & Mech, L.D. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Can. J. Zool. 72: 1557-1565.

44. Testa, J.W., Becker, E.F. & Lee, G.R. 2000. Temporal patterns in the survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. J. Mammal. 81: 162-168.
doi:10.1644/1545-1542(2000)081<0162:TPITSO>2.0.CO;2

45. Bertram, M.R. & Vivion, M.T. 2002. Moose mortality in eastern interior Alaska. J. Wildl. Manage. 66: 747-756.
doi:10.2307/3803140

46. Zager, P., White, C. & Pauley, G. 2005. Elk ecology. Study IV. Factors influencing elk calf recruitment. Job #s 1-3. Pregnancy rates and condition of cow elk. Calf mortality causes and rates. Predation effects on elk calf recruitment. Federal Aid in Wildlife Restoration, Job Progress Report, W-160-R-32. Idaho Department of Fish and Game, Boise, Idaho, USA.

47. Barber-Meyer, S.M., Mech, L.D. & White, P.J. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildl. Monogr. 169: 1-30.
doi:10.2193/2008-004

48. Pemberton, J.M., Albon, S.D., Guinness, F.E., Clutton-Brock, T.H. & Berry, R.J. 1988. Genetic variation and juvenile survival in red deer. Evolution 42: 921-934.
doi:10.2307/2408908

49. Coulson, T.N., Pemberton, J.M., Albon, S.D., Beaumont, M., Marshall, T.C., Slate, J., Guinness, F.E. & Clutton-Brock, T.H. 1998. Microsatellites reveal heterosis in red deer. Proc. R. Soc. Lond., B 265: 489-495.
doi:10.1098/rspb.1998.0321

50. Bossdorf, O., Richards, C.L., & Pigliucci, M. 2008. Epigenetics for ecologists. Ecol. Lett. 11: 106-115.

51. Crews, D., Gore, A.C., Hsu, T.S., Dangleben, N.L., Spinetta, M., Schallert, T., Anway, M.D., & Skinner, M.K. 2007. Transgenerational epigenetic imprints on mate preference. Proc. Natl. Acad. Sci., USA 104: 5942-5946.
doi:10.1073/pnas.0610410104

52. LeResche, R., Seal, U., Karns, P. & Franzmann, A. 1974. A review of blood chemistry of moose and other cervidae with emphasis on nutritional assessment. Nat. Can. 101: 263-290.

53. DelGiudice, G.D., Mech, L.D., Kunkel, K.E., Gese, E.M. & Seal, U.S. 1992. Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female white-tailed deer in Minnesota. Can. J. Zool. 70: 974-983.

54. Franzmann, A.W. & Thorne, E.T. 1970. Physiologic values in wild bighorn sheep (*Ovis canadensis canadensis*) at capture, after handling, and after captivity. J. Amer. Vet. Med. Ass. 157: 647-650.

55. Seal, U.S., Ozoga, J.J., Erickson, A.W. & Verme, L.J. 1972. Effects of immobilization on blood analyses of white-tailed deer. J. Wildl. Manage. 36: 1034-1040.
doi:10.2307/3799230

56. Franzmann, A.W., Flynn, A. & Arneson, P.D. 1975. Serum corticoid levels relative to handling stress in Alaskan moose. Can. J. Zool. 53: 1424-1426.

57. Franzmann, A.W. & LeResche, R.E. 1978. Alaskan moose studies with emphasis on condition evaluation. J. Wildl. Manage. 42: 334-351.
doi:10.2307/3800270

58. Seal, U.S., Nelson, M.E., Mech, L.D. & Hoskinson, R.L. 1978a. Metabolic indicators of habitat differences in four Minnesota deer populations. J. Wildl. Manage. 42: 746-754.
doi:10.2307/3800765

59. Wesson, J.A., Scanlon, P.F., Kirkpatrick, R.L. & Mosby, H.S. 1979. Influence of chemical immobilization and physical restraint on packed cell volume, total protein, glucose and blood urea nitrogen in blood of white-tailed deer. Can. J. Zool. 57: 756-767.

60. Hamlin, K.L. & Ross, M.S. 2002. Effects of hunting regulation changes on elk and hunters in the Gravelly-Snowcrest Mountains, Montana. Federal Aid Project W-120-R. April 2002. Montana Fish, Wildlife and Parks, Wildlife Division, Helena, Montana, USA.

61. Kie, J.G., White, M. & Drawe, D.L. 1983. Condition parameters of white-tailed deer in Texas. J. Wildl. Manage. 47: 583-594.
   doi:10.2307/3808596

62. Kirkpatrick, R.L., Buckland, D.E., Abler, W.A., Scanlon, P.F., Whelan, J.B. & Burkhart, H.E. 1975. Energy and protein influences on blood urea nitrogen of white-tailed deer fawns. J. Wildl. Manage. 39: 692-698.
   doi:10.2307/3800229

63. Seal, U.S. & Hoskinson, R.L. 1978. Metabolic indicators of habitat condition and capture stress in pronghorns. J. Wildl. Manage. 42: 755-763.
   doi:10.2307/3800766

64. Weber, B.J., Wolfe, M.L., White, G.C. & Rowland, M.M. 1984. Physiologic response of elk to differences in winter range quality. J. Wildl. Manage. 48: 248-253.
   doi:10.2307/3808482

65. Carstensen, M, DelGiudice, G.D., Sampson, B.A. & Kuehn, D.W. (In press). Survival and cause-specific mortality of white-tailed deer neonates relative to winter severity and nutritional condition of their dams. J. Wildl. Manage.

66. Sams, M.G., Lochmiller, R.L., Hellgren, E.C., Peyton, M.E. & Varner, L.W. 1995. Physiological responses of neonatal white-tailed deer reflective of maternal dietary protein intake. Can. J. Zool. 73: 1928-1936.

67. Seal, U.S., Verme, L.J. & Ozoga, J.J. 1978b. Dietary protein and energy effects on deer fawn metabolic patterns. J. Wildl. Manage. 42: 776-790.
   doi:10.2307/3800768

68. Smith, B.L., Williams, E.S., McFarland, K.C., McDonald, T.L., Wang, G. & Moore, T.D. 2006. Neonatal mortality of elk in Wyoming: environmental, population, and predator effects. U.S. Department of Interior, U.S. Fish and Wildlife Service, Biological Technical Publication Series, BTP-R6007-2006, Washington, D.C.

69. Blecha, F. & Kelley, K.W. 1981. Effects of cold and weaning stressors on the antibody-mediated immune response of pigs. J. Anim. Sci. 53: 439-447.

70. Findlay, C.R. 1973. Serum immune globulin levels in lambs under a week old. Vet. Rec. 92: 530-532.

71. Harker, D.B. 1974. Serum immune globulin levels in artificially reared lambs. Vet. Rec. 95: 229-231.

72. Logan, E.F. & Gibson, T. 1975. Serum immunoglobulin levels in suckled beef calves. Vet. Rec. 97: 229-230.

73. McGuire, T.C., Pfeiffer, N.E., Weikel, J.M. & Gartsch, R.C. 1976. Failure of colostral immunoglobulin transfer in calves dying from infectious disease. J. Amer. Vet. Med. Ass. 169: 713-718.

74. Vihan, V.S. 1988. Immunoglobulin levels and their effect on neonatal survival in sheep and goats. Small Ruminant Res. 1: 135-144.
   doi:10.1016/0921-4488(88)90029-6

75. Sams, M.G., Lochmiller, R.L., Qualls Jr., C.W., Leslie Jr., D.M. & Payton, M.E. 1996. Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. J. Mammal. 77: 179-190.
   doi:10.2307/1382719

76. Cook, J.G. 2002: Nutrition and food. In: Toweill, D.E. & Thomas, J.W. (eds.). North American elk ecology and management. Smithsonian Institution Press, Washington and London, pp. 259-349.

77. Cook, J.G., Irwin, L.L., Bryant, L.D., Riggs, R.A., Hengel, D.A. & Thomas, J.W. 1994. Studies of elk biology in northeast Oregon. 1993 Progress Report - National Council of the Paper Industry for Air and Stream Improvement, Corvallis, Oregon, USA.

78. Wolkers, J., Wensing, T. & Schonewille, J.T. 1994. Effect of undernutrition on haematological and serum biochemical characteristics in red deer (*Cervus elaphus*). Can. J. Zool. 72: 1291-1296. doi:10.1139/z94-172

79. Center, S.A., Randolph, J.F., ManWarren, T. & Slater, M. 1991. Effect of colostrum ingestion on gamma-glutamytransferase and alkaline phosphatase activities in neonatal pups. Am. J. Vet. Res. 52: 499-504.

80. Pauli, J.V. 1983. Colostral transfer of gamma glutamyl transferase in lambs. New Zeal. Vet. J. 31: 150-151.

81. Parkinson, D.E., Ellis, R.P. & Lewis, L.D. 1982. Colostrum deficiency in mule deer fawns: identification, treatment and influence on neonatal mortality. J. Wildl. Dis. 18: 17-28.

82. DelGiudice, G.D., Mech, L.D., Seal, U.S. & Karns, P.D. 1987. Effects of winter fasting and refeeding on white-tailed deer blood profiles. J. Wildl. Manage. 51: 865-873. doi:10.2307/3801753

83. DelGiudice, G.D., Mech, L.D. & Seal, U.S. 1990. Effects of winter undernutrition on body composition and physiological profiles of white-tailed deer. J. Wildl. Manage. 54: 539-550. doi:10.2307/3809347

84. Harder, J.D. & Kirkpatrick, R.L. 1994. Physiological methods in wildlife research. In: Bookhout, T.A. (ed.). Research and management techniques for wildlife and habitats, 5th ed. The Wildlife Society, Bethesda, Maryland, USA, pp. 275-306.

85. Bowden, D.C. 1971. Non-esterified fatty acids and ketone bodies in blood as indicators of nutritional status in ruminants: a review. Can. J. Anim. Sci. 51: 1-13.

86. Thurley, D.C. & McNatty, K.P. 1973. Factors affecting peripheral cortisol levels in unrestricted ewes. Acta Endocrinol (Copenh) 74: 331-337.

87. Seal, U.S., Verme, L.J. & Ozoga, J.J. 1981. Physiologic values. In: Davidson, W.R. (ed.); Disease and parasites of white-tailed deer. Tall Timbers Research Station, Tallahassee, Florida, USA, pp. 17-34.

88. Saltz, D. & White, G.C. 1991. Urinary cortisol and urea nitrogen responses to winter stress in mule deer. J. Wildl. Manage. 55: 1-16. doi:10.2307/3809235

89. Remick, D. & Friedland, J. (eds.). 1997. Cytokines in health and disease, 2nd ed. Dekker, New York, USA.

90. Beutler, B. & Cerami, A. 1989. The biology of cachectin / TNF-alpha: primary mediator of the host response. Annu. Rev. Immunol. 7: 625-655.

91. Spaulding, C.C., Walford, R.L. & Effros, R.B. 1997. Calorie restriction inhibits the age-related dysregulation of the cytokines TNF-$\alpha$ and IL-6 in C3B10RF1 mice. Mech. Ageing Dev. 93: 87-94. doi:10.1016/S0047-6374(96)01824-6

92. Ditchkoff, S.S., Sams, M.G., Lochmiller, R.L. & Leslie Jr., D.M. 2001. Utility of tumor necrosis factor-$\alpha$ and interleukin-6 as predictors of neonatal mortality in white-tailed deer. J. Mammal. 82: 239-245. doi:10.1644/1545-1542(2001)082<0239:UOTNFA>2.0.CO;2

93. Pojar, T.M. & Bowden, D.C. 2004. Neonatal mule deer fawn survival in west-central Colorado. J. Wildl. Manage. 68: 550-560. doi:10.2193/0022-541X(2004)068[0550:NMDFSI]2.0.CO;2

94. Verme, L.J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Proc. Natl. White-tailed Deer Disease Symp. 1: 15-38.

95. Singer, F.J., Harting, A., Symonds, K.K., & Coughenour, M.B. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. J. Wildl. Manage. 61: 12-25.
doi:10.2307/3802410

96. Nelson, T.A. & Woolf, A. 1987. Mortality of white-tailed deer fawns in southern Illinois. J. Wildl. Manage. 51: 326-329.
doi:10.2307/3801010

97. Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W. & Stephenson, T.R. 2000. Life-history consequences of maternal condition in Alaskan moose. J. Wildl. Manage. 64: 450-462.
doi:10.2307/3803243

98. Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. N. Y. State Conserv. 3: 19-22.

99. Goudreault, F. 1977. Physiological response of deer to winter stress in Quebec as determined by femur fat content. In: Potvin, F. & Huot, J. (eds.). Northeastern deer study group meeting. Ministered du Loisir, de la Chasse et de la Peche, du Quebec, pp. 37-55.

100. Mech, L.D. 2007. Femur-marrow fat of white-tailed deer fawns killed by wolves. J. Wildl. Manage. 71: 920-923.
doi:10.2193/2006-153

101. Adams, L.G. 2003. Marrow fat deposition and skeletal growth in caribou calves. J. Wildl. Manage. 67: 20-24.
doi:10.2307/3803057

102. Testa, J.W. & Adams, L.G. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). J. Mammal. 79: 1345-1354.
doi:10.2307/1383026

103. Mech, L.D., Nelson, M.E. & McRoberts, R.E. 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. J. Mammal. 72: 146-151.
doi:10.2307/1381989

104. Bergerud, A.T. 1974. The role of environment in the aggregation, movement and disturbance behaviour of the caribou. In: Geist, V. & Walthers, F. (eds.). The behaviour of ungulates and its relationship to management: the papers of an international symposium. University of Calgary, Alberta, Canada, November 2-5, 1972. IUCN, Morges, Switzerland, pp. 552-584.

105. Ims, R.A. 1990. The ecology and evolution of reproductive synchrony. Trends Ecol. Evol. 5: 135-140.
doi:10.1016/0169-5347(90)90218-3

106. Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). J. Zool., Lond. 214: 653-661.

107. Côté, S.D. & Festa-Bianchet, M. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127: 230-238.
doi:10.1007/s004420000584

108. Guinness, F.E., Clutton-Brock, T.H., & Albon, S.D. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). J. Anim. Ecol. 47: 817-832.
doi:10.2307/3673

109. Bunnell, F.L. 1982. The lambing period of mountain sheep: synthesis, hypothesis, and tests. Can. J. Zool. 60: 1-4.

110. Linnell, J.D.C. & Andersen, R. 1998. Timing and synchrony of birth in a hider species, the roe deer Capreolus capreolus. J. Zool. 244: 497-504.
doi:10.1111/j.1469-7998.1998.tb00055.x

111. Aanes, R. & Andersen, R. 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. Can. J. Zool. 74: 1857-1865. doi:10.1139/z96-209

112. Darling, F.F. 1938. Bird flocks and breeding cycle. Cambridge University Press, Cambridge.

113. Pulliam, H.R. & Caraco, T.R. 1984. Living in groups: is there an optimal group size? In: Krebs, J.R. & Davies, N.B. (eds.). Behavioural ecology: an evolutionary approach, 2nd ed. Sinauer, Sunderland, Massachusetts, USA, pp. 122-147.

114. Rutberg, A.T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. Am. Nat. 130: 692-710. doi:10.1086/284739

115. Hamilton, W.D. 1971. The geometry of the selfish herd. J. Theor. Biol. 31: 295-311. doi:10.1016/0022-5193(71)90189-5

116. Kruuk, H. 1964. Predators and anti-predation behavior of the black-headed gull (*Larus ridibundus*). Behaviour, Supplement 11. Brill, Leiden, 129 pp.

117. Estes, R.D. & Estes, R.K. 1979. The birth and survival of wildebeest calves. Z. Tierpsychol. 50: 45-95.

118. Wissel, C. & Brandl, R. 1988. A model for the adaptive significance of partial reproductive synchrony within social units. Evol. Ecol. 2: 102-114. doi:10.1007/BF02067271

119. Mitchell, B. & Lincoln, G.A. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. J. Zool. 171: 141-152.

120. Reimers, E., Klein, D.R. & Soerumgaard, R. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. Arctic Alpine Res. 15: 107-118. doi:10.2307/1550986

121. Ozoga, J.J., Verme, L.J. & Bienz, C.S. 1982. Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. J. Wildl. Manage. 46: 1-11. doi:10.2307/3808402

122. Ozoga, J. J. & Verme, L.J. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. J. Wildl. Manage. 50: 480-486. doi:10.2307/3801110

123. Mech, L.D. & McRoberts, R.E. 1990. Survival of white-tailed deer fawns in relation to maternal age. J. Mammal. 71: 465-467. doi:10.2307/1381963

124. Nixon, C.M. & Etter, D. 1995. Maternal age and fawn rearing success for white-tailed deer in Illinois. Am. Midl. Nat. 133: 290-297. doi:10.2307/2426393

125. Dekker, D., Bradford, W. & Gunson, J.R. 1995. Elk and wolves in Jasper National Park, Alberta, from historical times to 1992. In Carbyn, L.N., Fritts, S.H. & Seip, D.R. (eds.). Ecology and conservation of wolves in a changing world (Occasional Publication No. 35). Canadian Circumpolar Institute, Edmonton, Alberta, Canada, pp. 85-94.

126. Barton, N.H. & Keightley, P.D. 2002. Understanding quantitative genetic variation. Nat. Rev. Genet. 3: 11-20. doi:10.1038/nrg700

127. Gustafsson, L. 1986. Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. Am. Nat. 128: 761-764. doi:10.1086/284601

128. Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426: 655-658. doi:10.1038/nature02177

129. Cheverud, J.M. & Buikstra, J.E. 1982. Quantitative genetics of skeletal nonmetric traits in the rhesus macaques of Cayo Santiago. III. Relative heritability of skeletal nonmetric and metric traits. Am. J. Phys. Anthropol. 59: 151-155.
doi:10.1002/ajpa.1330590205

130. Plomin, R., DeFries, J.C., McClearn, G.E. & Rutter, M. 1997. Behavioral genetics, 3rd ed. W. H. Freeman and Company, New York, USA.

131. Gershenfeld, H.K., Neumann, P.E., Mathis, C., Crawley, J.N., Li, X. & Paul, S.M. 1997. Mapping quantitative trait loci for open-field behavior in mice. Behav. Genet. 27: 201-210.
doi:10.1023/A:1025653812535

132. Burrow, H.M. 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. Livest. Prod. Sci. 70: 213-233.
doi:10.1016/S0301-6226(01)00178-6

133. Prayaga, K.C., & Henshall, J.M. 2005. Adaptability in tropical beef cattle: genetic parameters of growth, adaptive and temperament traits in a crossbred population. Aust. J. Exp. Agr. 45: 971-983.
doi:10.1071/EA05045

134. Saudino, K.J. & Plomin, R. 1996. Personality and behavioral genetics: where have we been and where are we going? J. Res. Personality 30: 335-347.
doi:10.1006/jrpe.1996.0023

135. Peripato, A.C. & Cheverud, J.M. 2002. Genetic influences on maternal care. Am. Nat. 160: S173-S185.
doi:10.1086/342900

136. Chen, C., Rainnie, D.G., Greene, R.W. & Tonegawa, S. 1994. Abnormal fear response and aggressive behavior in mutant mice deficient for alpha-calcium-calmodulin kinase II. Science 14: 291-294.
doi:10.1126/science.7939668

137. Clement, Y., Kia, K.H., Daval, G. & Verge, D. 1996. An autoradiographic study of serotonergic receptors in a murine genetic model of anxiety-related behaviors. Brain Res. 709: 229-242.
doi:10.1016/0006-8993(95)01297-4

138. Murray, K., Thompson, S.D., & Glass, D.N. 1997. Pathogenesis of juvenile chronic arthritis: genetic and environmental factors. Arch. Dis. Child. 77: 530-534.

139. Prahalad, S. 2004. Genetics of juvenile idiopathic arthritis: an update. Curr. Opin. Rheumatol. 16: 588-594.
doi:10.1097/01.bor.0000134407.48586.b0

140. Sekulic, R. 1978. Seasonality of reproduction in sable antelope. E. Afr. Wildl. J. 16: 177-182.

141. Walther, F. 1960. Einige Verhaltensbeobachtungen am Bergwild des Georg von Opel-Freigeheges. [Some behavioral observations on Chamois in the Georg von Opel-Enclosure]. Jahrb. G. v. Opel Freigehege. Tierforsch. 3: 53-89.

142. Walther, F. 1964. Verhaltensstudien an der Gattung Tragelaphus De Blainville, 1816, unter besonderer Beruecksichtigung des Sozialverhaltens. [Behavioral studies on the genus Tragelaphus De Blainville, 1816, under special consideration of the social behavior]. Z. Tierpsychol. 21: 393-467.

143. Walther, F. 1968. Verhalten Der Gazellen. [Behavior of gazelles]. Wittenberg-Lutherstadt, A. Ziemsen Verlag.

144. Lent, P.C. 1974. Mother-infant relationships in ungulates. In: Geist, V. & Walther, F. (eds.). The behaviour of ungulates and its relation to management. International Union for the Conservation of Nature, Morges, Switzerland, pp. 14-55.

145. Bubenik, A.B. 1965. Beiträge zur geburtskunde und zu den mutter-kind beziehungen des reh (*Capreolus capreolus* L.) und rotwildes (*Cervus elaphus* L.). [Contribution to the knowledge of birth and adult female juvenile relationship of the roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.)]. Z. Säugetierkd. 30: 65-128.

146. Geist, V. 2002. Adaptive behavioral strategies. In: Toweill, D.E. & Thomas, J.W. (eds.). North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA, pp. 389-433.

147. Wallace, M.C. & Krausman, P.R. 1991. Neonatal elk habitat in central Arizona. In: Brown, R.D. (ed.). The biology of deer. Springer-Verlag, New York, USA, pp. 69-75.

148. White, K.S. & Berger, J. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? Can. J. Zool. 79: 2055-2062.
doi:10.1139/cjz-79-11-2055

149. Dehn, M.M. 1990. Vigilance for predators: detection and dilution effects. Behav. Ecol. Sociobiol. 26: 337-342.

150. Laundré, J.W., Hernández, L. & Altendorf, K.B. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Can. J. Zool. 79: 1401-1409.
doi:10.1139/cjz-79-8-1401

151. Smythe, N. 1970. On the existence of "pursuit invitation" signals in mammals. Am. Nat. 104: 491-494.
doi:10.1086/282684

152. Smythe, N. 1977. The function of mammalian alarm advertising: social signals or pursuit invitation? Am. Nat. 111: 191-194.
doi:10.1086/283149

153. Guthrie, R.D. 1971. A new theory of mammalian rump patch evolution. Behaviour 38: 132-145.
doi:10.1163/156853971X00041

154. Berger, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behav. Ecol. Sociobiol. 4: 91-99.
doi:10.1007/BF00302563

155. Bildstein, K.L. 1983. Why white-tailed deer flag their tails. Am. Nat. 121: 709-715.
doi:10.1086/284096

156. LaGory, K.E. 1986. Habitat, group size, and the behaviour of white-tailed deer. Behaviour 98: 168-179.
doi:10.1163/156853986X00955

157. Gray, D.R. 1987. The muskoxen of Polar Bear Pass. Fitzhenry and Whiteside, Markham, Ontario.

158. Caro, T.M., Lombardo, L., Goldizen, A.W. & Kelly, M. 1995. Tail-flagging and other antipredator signals in white-tailed deer: new data and synthesis. Behav. Ecol. 6: 442-450.
doi:10.1093/beheco/6.4.442

159. Murie, A. 1944. The wolves of Mt. McKinley. U.S. National Park Service Fauna Series, no. 5. U.S. Government Printing Office, Washington, D.C.

160. Cowan, I.M. 1947. The timber wolf in the Rocky Mountain national parks of Canada. Can. J. Res. 25D: 139-174.

161. Peterson, R.L. 1955. North American moose. University of Toronto Press, Toronto.

162. Crisler, L. 1956. Observations of wolves hunting caribou. J. Mammal. 37: 337-346.
doi:10.2307/1376732

163. Mech, L.D. 1966. The wolves of Isle Royale. Government Printing Office, Washington, D.C., USA.

164. Grundlach, H. 1968. Brutvorsorge, Brutpflege, Verhaltensontogenese and Tagesperiodik beim europaischen Wildschwein (*Sus scrofa* L.). [Provision and care of the brood, behavioral ontogenesis and Tagesperiodik (diurnal rhythm) of the European Wild Boar (*Sus scrofa* L.)]. Z. Tierpsychol. 25: 955-995.

165. Carbyn, L.N. 1974. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey diversity. Canadian Wildlife Service, Edmonton, Alberta.

166. Rideout, C.B. 1978. Mountain goat. In: Schmidt, J.L. & Gilbert, D.L. (eds.). Big game of North America: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA, pp. 149-159.

167. Nelson, M. & Mech, L.D. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. 77: 1-53.

168. Stephens, P.W. & Peterson, R.O. 1984. Wolf avoidance strategies of moose. Holarctic Ecol. 7: 239-244.

169. Bergerud, A.T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Can. J. Zool. 63: 1324-1329.

170. Fox, J.L. & Streveler, G.P. 1986. Wolf predation on mountain goats in southeastern Alaska. J. Mammal. 67: 192-195.
doi:10.2307/1381024

171. Sumanik, R.S. 1987. Wolf ecology in the Kluane Region, Yukon Territory. M.S. Thesis, Michigan Technical University, Houghton, Michigan, USA.

172. Darling, F.F. 1937. A herd of red deer. Oxford University Press, London, United Kingdom.

173. Holroyd, J.D. 1967. Observations of Rocky Mountain goats on Mount Wardle, Kootenay National Park, British Columbia. Can. Field Nat. 81: 1-22.

174. Kitchen, D.W. 1974. Social behavior and ecology of the pronghorn. Wildl. Monogr. 38: 1-96.

175. Bergerud, A.T., Butler, H.E., and Miller, D.R. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Can. J. Zool. 62: 1566-1575.

176. Heard, D.C. 1992. The effect of wolf predation and snow cover on musk-ox group size. Am. Nat. 139: 190-204.
doi:10.1086/285320

177. Carbyn, L.N., Oosenbrug, S.M. & Anions, D.W. 1993. Wolves, bison and the dynamics related to the Peace Athabaska Delta in Canada's Wood Buffalo National Park. Circumpolar Research Series, no. 4. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

178. Hebblewhite, M., & Pletscher, D.H. 2002. Effects of elk group size on predation by wolves. Can. J. Zool. 80: 800-809.
doi:10.1139/z02-059

179. Roe, F.G. 1951. The North American buffalo: a critical study of the species in its wild state. University of Toronto Press, Toronto.

180. Hediger, H. 1955. The psychology and behavior of animals in zoos and circuses. Dover, New York, USA.

181. Geist, V. 1982. Adaptive behavioral strategies. In: Thomas, J.W. & Toweill, D.E. (eds.). North American elk: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA, pp. 219-278.

182. Walther, F. 1984. Communication and expression in hoofed mammals. Bloomington, Indiana University Press, Indiana, USA.

183. Thompson, K.V. 1996. Maternal strategies in sable antelope *Hippotragus niger*: factors affecting variability in maternal retrieval of hiding calves. Zoo Biol. 15: 555-564.
doi:10.1002/(SICI)1098-2361(1996)15:6<555::AID-ZOO2>3.0.CO;2-A

184. Youngson, R.W. 1970. Rearing red deer calves in captivity. J. Wildl. Manage. 34: 467-470.
doi:10.2307/3799037

185. Arman, P. 1974. A note on parturition and maternal behavior in captive red deer (*Cervus elaphus* L.). J. Reprod. Fertil. 37: 87-90.
doi:10.1530/jrf.0.0370087

186. Hoskinson, R.L. & Mech, L.D. 1976. White-tailed deer migration and its role in wolf predation. J. Wildl. Manage. 40: 429-441.
doi:10.2307/3799944

187. Mech, L.D. 1977a. Population trend and winter deer consumption in a Minnesota wolf pack. In: Phillips, R.L. & Jonkel, C. (eds.). Proceedings of the 1975 predator symposium. Montana Forest and Conservation Experiment Station, University of Montana, Missoula, USA, pp. 55-83.

188. Mech, L.D. 1977b. Wolf-pack buffer zones as prey reservoirs. Science 198: 320-321. doi:10.1126/science.198.4314.320

189. Franklin, W.L. & Lieg, J.W. 1978. The social organization of a sedentary population of North American elk: a model for understanding other populations. In: Boyce, M.S. & Hayden-Wing, L.D. (eds.). North American elk: ecology, behavior and management. University of Wyoming, Laramie, pp. 185-198.

190. Byers, J.A. & Byers, K.Z. 1983. Do pronghorn mothers reveal the locations of their hidden fawns? Behav. Ecol. Sociobiol. 13: 147-156. doi:10.1007/BF00293804

191. Altman, M. 1963. Naturalistic studies of maternal care in moose and elk. In: Rheingold, H.L. (ed.). Maternal behavior in mammals. J. Wiley and Sons, New York, USA, pp. 233-253.

192. FitzGibbon, C.D. 1993. Antipredator strategies of female Thomson's gazelles with hidden fawns. J. Mammal. 74: 758-762. doi:10.2307/1382299

193. Murie, O.L. 1951. The elk of North America. Stackpole Co., Harrisburg, Pennsylvania, USA.

194. Harper, J.A., Ham, J.H., Bentley, W.W. & Yocum, C.F. 1967. The status and ecology of the Roosevelt elk in California. Wildl. Monogr. 16: 1-49.

195. McCullough, D.R. 1969. The Tule elk: its history, behavior, and ecology. University of California Press Publications in Zoology, Berkeley, California, USA.

196. Dathe, H. 1966. Zum Mutter-Kind Verhalten bei Cerviden. [On mother-child behavior of Cervids]. Beitr. Jagd. Wildforsch. 5: 83-93.

197. Bromley, P.T. 1976. Aspects of the behavioral ecology and sociobiology of the pronghorn (*Antilocapra americana*). Ph.D. Thesis, University of Calgary, Alberta.

198. Walther, F., Mungall, E.C. & Grau, G.A. 1983. Gazelles and their relatives. A study in territorial behavior. Noyes Publication, Park Ridge, New Jersey, USA.

199. Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., & Quigley, H. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. Oikos 101: 591-601. doi:10.1034/j.1600-0706.2003.12230.x

200. Molinari-Jobin, A., Molinari, P., Loison, A., Gaillard, J.-M., & Breitenmoser, U. 2004. Life cycle period and activity of prey influence their susceptibility to predators. Ecography 27: 323-329. doi:10.1111/j.0906-7590.2004.03862.x