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Foraging and Feeding Ecology of the Gray Wolf (*Canis lupus*): Lessons from Yellowstone National Park, Wyoming, USA[1–3]

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ABSTRACT The foraging and feeding ecology of gray wolves is an essential component to understanding the role that top carnivores play in shaping the structure and function of terrestrial ecosystems. In Yellowstone National Park (YNP), predation studies on a highly visible, reintroduced population of wolves are increasing our understanding of this aspect of wolf ecology. Wolves in YNP feed primarily on elk, despite the presence of other ungulate species. Patterns of prey selection and kill rates in winter have varied seasonally each year from 1995 to 2004 and changed in recent years as the wolf population has become established. Wolves select elk based on their vulnerability as a result of age, sex, and season and therefore kill primarily calves, old cows, and bulls that have been weakened by winter. Summer scat analysis reveals an increased variety in diet compared with observed winter diets, including other ungulate species, rodents, and vegetation. Wolves in YNP hunt in packs and, upon a successful kill, share in the evisceration and consumption of highly nutritious organs first, followed by major muscle tissue, and eventually bone and hide. Wolves are adapted to a feast-or-famine foraging pattern, and YNP packs typically kill and consume an elk every 2–3 d. However, wolves in YNP have gone without fresh meat for several weeks by scavenging off old carcasses that consist mostly of bone and hide. As patterns of wolf density, prey density, weather, and vulnerability of prey change, in comparision with the conditions of the study period described here, we predict that there will also be significant changes in wolf predation patterns and feeding behavior. J. Nutr. 136: 1923S–1926S, 2006.

KEY WORDS: • *wolves* • *Canis lupus* • *foraging* • *predation* • *elk* • *Yellowstone National Park*

Since the 1920s, when the last of the wolves in Yellowstone National Park (YNP) were killed, these predators have been absent as an ecological force in the Greater Yellowstone Ecosystem (GYE). This ecosystem, however, evolved in the presence of large carnivores, as did most of the Northern Hemisphere. Wolf-like canids have been around for 50–60 million years, diverging early on from other carnivore families (1) and the first modern wolf appeared during the early Pleistocene era, ~1.8 million years ago (2). European settlers to North America eliminated wolves from most of the United States by the mid-twentieth century (3), disrupting a rich evolutionary history and altering the structure and function of ecosystems where wolves were present. Since that time, these ecosystems have been without a top predator. Recent studies indicate that large carnivores play highly important roles in the structuring of ecosystems, acting as a top-down influence (4–9).

The effort to restore wolves to the Rocky Mountain west took decades of government and public involvement, and culminated with the reintroduction of wolves to YNP in 1995 and 1996 (10). By 2005, a robust population had reestablished itself in the GYE and 10 years of research has begun to provide insight on the impact that wolf recovery is having on one of the few intact temperate ecosystems in the United States (11). In YNP, a main topic of research on wolves has focused largely on their role as a predator. Being a highly adaptive and behaviorally flexible carnivore, wolves have evolved to hunt prey ranging in size from 1 kg to 1000 kg, although they are most commonly categorized as cursorial hunters of large ungulates (12). As a result, much of the physical, behavioral, and ecological characteristics of wolves are directly related to their predation and feeding on large ungulates. This article describes various aspects of wolf foraging ecology and feeding behavior in a newly restored population.

MATERIALS AND METHODS

Other publications describe in detail the study area, reintroduction, marking, and field methods associated with the information provided in this article (10,13,14), so only a basic background is provided here. The GYE's 58,026 km^2 area is made up of mostly public land in Idaho, Montana, and Wyoming, with Yellowstone National Park (8991 km^2)

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as its center. Within YNP, there is a wide variation in elevation (1500–3800 m), precipitation (26–205 cm), and temperature (–40 to 30°C), which results in diverse habitat types ranging from grasslands to alpine, but forests predominate among a mosaic of riparian, lake, and thermal valleys (15). Most of the original flora and fauna present when YNP was established are still present, with wolves being the last extirpated carnivore restored (16). Few North American ecosystems have the array of large carnivores that are present in YNP: wolves, cougars (*Puma concolor*), coyotes (*Canis latrans*), and grizzly (*Ursus arctos*) and black bears (*Ursus americanus*). Also inhabiting YNP, all or part of the year, are elk (*Cervus elephus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*) (10,14,17).

Wolves from Alberta and British Columbia, Canada were reintroduced to YNP in 1995–1996 after an ~70-y absence (10). Starting from an original reintroduced population of 31 wolves, the population grew to 171 individuals living in 16 packs at the end of 2004 (18). At least 1 individual from each pack was marked with a radio collar, allowing packs to be tracked throughout the year from both aerial and ground monitoring. One of the primary methods for documenting wolf predation is by monitoring radio-marked wolf packs for 30 d in early (mid-November to mid-December) and late (March) winter from November 1995 through March 2004 [see (14) for details of these field methods]. Observations on predation and feeding behavior were made at every opportunity throughout the year outside of the biannual winter studies. Summer diet analysis was conducted through scat collection at summer den and rendezvous sites. Scat analysis (Big Sky Beetle Works, LLC) determined the percent occurrence of food types by species or categories in total number of scats analyzed. Although this does not provide biomass consumption, it is the standard technique for characterizing the wolf diet (19).

RESULTS

Wolves in YNP regularly kill and consume large ungulates for survival. Elk have been the primary prey of wolves since their reintroduction, despite the presence of 8 ungulate species. Of the 2347 documented ungulate kills by wolves between 1995–2003, 2,060 (88%) were elk (**Fig. 1**). During the 30-d early winter studies of 1995–2003, the proportion of elk calves, prime-age cows (1–9 y), old cows (>10 y), and bulls killed on the northern range of YNP by wolves was 142 (51%), 28 (10%), 55 (20%), and 52 (19%), respectively (**Fig. 2***A*). This pattern of elk sex and age selection by wolves is changing, however. During the same early winter study in 2004, the proportion of elk calves, prime-age cows, old cows, and bulls killed was 7 (18%), 10 (25%), 6 (15%), and 17 (43%), respectively (Fig. 2*B*). Yellowstone wolves also select for the older, senescent elk; the mean age of the wolf-killed adult cow elk for 1995–2004 was 13.4 ± 0.2 y (range, 1–26, $n = 434$).

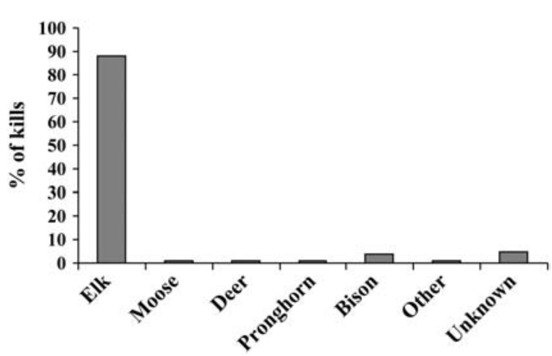

FIGURE 1 The percentage of the total number of major ungulate species documented as wolf-killed prey in winter in Yellowstone National Park from 1995–2003 ($n = 2347$).

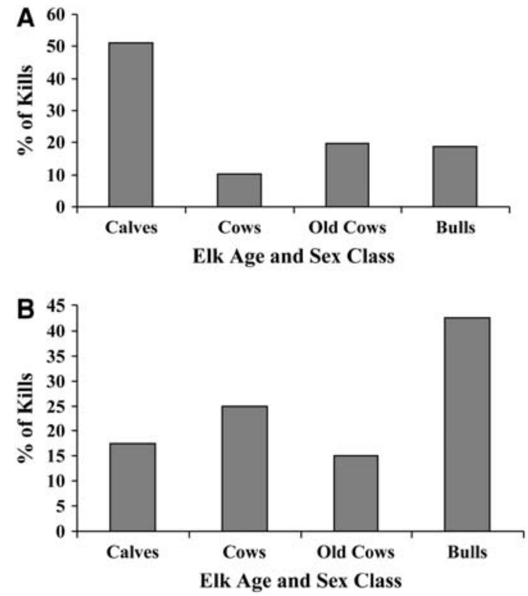

FIGURE 2 The percentage of each age and sex category for the total number of wolf-killed elk detected during the November–December winter studies on Yellowstone's northern range for 1995–2003 ($n = 277$) (*A*) and 2004 ($n = 40$) (*B*). For these categories, cows are defined as 1–9 y old, whereas old cows are defined as >10 y old. The bulls category includes all age classes >1 y of age.

The frequency with which wolves kill elk varies by season. Early in the winter, when prey are in good condition and harder for the wolves to bring down, the rate at which they take prey is usually less than in late winter. During the first 5 y after restoration (1995–2000), each wolf killed a mean of 1.6 elk over 30 d in early winter, and 2.2 elk during a 30-d period in late winter, for a winter mean of 1.9 elk/wolf every 30 d (14). However, since ~2000, wolf kill rates have not increased in late winter, and overall, wolves are killing fewer elk (1.1 elk/wolf every 30 d from 2000 to 2004). These patterns of seasonal and annual killing frequencies are also seen when calculating ungulates · pack^{-1} · d^{-1}. Early on, wolves killed more frequently in late winter than early winter, a trend no longer true for 2000–2004 (**Fig. 3**).

As most of our information on wolf kills comes from winter data, kill rates and prey selection are less known in summer.

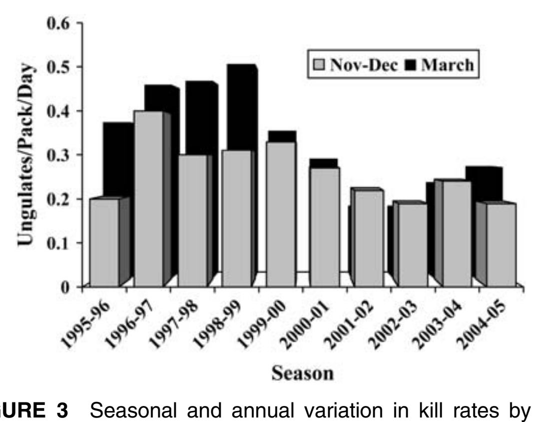

FIGURE 3 Seasonal and annual variation in kill rates by wolves expressed as ungulates killed · wolf pack^{-1} · d^{-1} for the early winter (November–December) and late winter (March) study periods of 1995–2005. Values shown are minimum kill rates documented for wolf packs living in the northern range of Yellowstone National Park.

Current studies exploring this aspect of wolf predation are under way, but preliminary evidence indicates that wolf kill rates decrease as much as 25% in the summer (D. Smith and D. Stahler, Yellowstone Wolf Project, unpublished data). One indication of the seasonal differences in wolf foraging patterns is through an analysis of summer wolf scats. Scat analysis shows that summer diets are more diverse and include smaller prey species such as rodents, birds, and invertebrates, as well as ungulates, otherwise absent in the winter. Analyses of summer scats in 2003 show that mule deer was present in 133 (25%) of 530 scats analyzed. In addition, plant matter is prevalent in wolves' summer diet, with 392 (74%) of 530 scats analyzed containing some type of plant material, largely grass (Graminae). This is consistent with summer observations of wolves consuming grass and other plant material.

As social carnivores, wolves in YNP most commonly hunt elk as a pack, with 2–3 wolves typically involved in the actual killing. When hunting elk, wolves attack an individual, or chase groups to select an individual that is vulnerable enough to kill. Prey that run are more likely to be killed by wolves than those that stand their ground. The neck is a common attack point on calves and cow elk, unlike larger bulls, which are more likely to be attacked from behind. Immediately after killing an elk, wolves open the body cavity, using their canines and incisors, and remove and consume the internal organs such as the heart, lungs, liver, intestines, spleen, and kidneys. Consumed next are the large muscle masses of each leg. Wolves consume up to 10 kg of meat during initial feeding bouts and then rest in close proximity to the carcass for several hours before feeding again. With organs and major muscle mass consumed, wolves then pick the remaining tissue off ribs, leg bones, and hide. Using their carnassials to shear remaining meat and crush hard-to-chew materials such as bone, tendon, cartilage, and hide, wolves continue to obtain nutritional derivatives from virtually all parts of ungulate carcasses. Wolves do not feed on the contents of the rumen; so this, along with the larger unbreakable bones and some of the hide, are often the only things remaining when wolves and associated scavengers are done. In YNP, where wolf and scavenger density is high, carcasses rarely last >48 h on the landscape.

With respect to the food requirements for wild wolves, a minimum daily energy requirement of 3.25 kg $\cdot$ wolf$^{-1} \cdot$ d^{-1} (5 × daily basal metabolic rate) has been estimated for a 35 kg wolf (12). For wolves in YNP (mean wt 45 kg), estimated mean food consumption rates based on early and later winter kill rates is 5.7 kg $\cdot$ wolf$^{-1} \cdot$ d^{-1} and 10.4 kg $\cdot$ wolf$^{-1} \cdot$ d^{-1}, respectively. Actual consumption rates are less than this, however, because these values are based on live weights of respective age and sex class of ungulates killed and do not take into account biomass lost to scavengers or inedible rumen or bone. Adapted to a feast-or-famine foraging pattern, a pack of wolves typically kills and consumes an elk every 2–3 d in Yellowstone. This adaptation allows wolves to sustain long periods without fresh meat. For example, in the summer of 2005, a lone wolf in YNP was followed for 10 wk using a downloadable GPS (global positioning satellite) collar providing locations at 30 min intervals. Upon close investigation of the wolf's movements and clustered locations, there was no evidence of it making a kill. The GPS data showed, however, that the wolf survived by scavenging over 10 carcasses ranging from 2 wk to 4 mo old, most of which consisted of only bone and hide.

DISCUSSION

In YNP, patterns of predation by wolves show that they do not kill at random but select their prey for species, age, and sex while foraging. Wolves do not attack prey at random because the risk of injury and death is too high. Therefore, as selective foragers, wolves in YNP search for vulnerable prey and must be risk aversive (14,20). Due to the greater density of elk compared with any other ungulate species in YNP (21) and the relative trade-offs between encounter rate, the risk of injury, and hunting success involved with killing elk vs. other ungulates in the system (20), wolves select them over other available ungulate species. Seasonally, there is strong selection for calves, which comprised 18% of the available elk between 1995 and 2000 (14). Young elk are likely more vulnerable just because they are young, which makes them easier to catch and kill than adults. There was also strong selection against cows, as they comprised ~60% of the available elk for the same time period. However, when cows are killed, wolves select older individuals that are presumably easier to kill than those in their prime (ages 1–9 y). For the period of 1995–2000, wolves killed bulls in proportion to their availability. The switch from calf to bull selection seen in the early winter of 2004 is notable, as are the declining kill rates and their seasonal variation for 2000–2004. Differences in seasonal kill rates for 1995–2000 are likely explained by differences in elk vulnerability. The changing trends in kill rates, seasonal variation, and prey selection are less understood at this time, but are likely the result of a combination of factors: availability and vulnerability of prey, interference competition between wolf packs, and winter severity and drought (D. Smith and D. Stahler, Yellowstone Wolf Project, unpublished data).

In summer, the combination of divided hunting units, smaller prey, more widely distributed prey on larger summer ranges, and greater activity at night, makes understanding wolf predation difficult. Although, as scat analysis reveals, we documented a greater variety in the summer diet as more food types become seasonally available. Because summer conditions lower individual energy requirements for most wolves (lactating females may be an exception), ongoing studies indicate that wolves kill fewer ungulates during the summer in YNP (D. Smith and D. Stahler, Yellowstone Wolf Project, unpublished data). The prevalence of vegetation found in summer scats indicates that consumption of these food types is intentional; it has been suggested that this may serve as an added source of vitamins or may aid in eradicating intestinal parasites (22).

Much of the foraging ecology of wolves is influenced by their degree of sociality. Wolves are territorial mammals that establish firm boundaries that they defend against other wolves (22). These territories are defended by a family of wolves, a pack, which is the basic structure of wolf society. There are 2 kinds of pack structures in YNP: simple and complex. Simple packs are made up of a breeding pair with pups; a complex pack is a breeding pair with several generations of offspring or unrelated individuals. In Yellowstone, where wolves feed largely on mid-sized elk, the mean pack size over the first 10 y has been 11 wolves, but the range of pack sizes was 2–37 (11). Complex packs have more experienced individuals, which aides in hunting success and food provisioning to pups in the summer, but also results in higher levels of intra-pack competition for food. The degree to which wolves share food at carcass locations depends on a variety of ecological and social factors, but previous wild and captive studies suggest a high degree of competition and a structured feeding hierarchy at these locations (23,24). In Yellowstone, feeding opportunity seems restricted only to the availability of a position to obtain meat from a carcass, and we see little social tension between age and sex groups at carcass locations. This is likely due to the fact that the ecosystem still offers a high prey density and therefore little food stress at this time.

Wolves can lose significant amounts of biomass from their kills to scavenger species such as ravens (*Corvus corax*), black-billed magpies (*Pica pica*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaeetus leucocephalus*), coyotes (*Canis latrans*), and grizzly bears (*Ursus arctos*) that closely associate with them and their carcasses (25–27). Other studies indicate that larger wolf packs accrue foraging advantages over smaller packs by losing less to scavengers (27,28). Wolves typically utilize most parts of an ungulate carcass, which is essential for their nutritional demands. Organs such as the heart, lungs, liver, and kidneys are high in B vitamins, vitamin A, minerals, and fatty acids that are required for maintenance, growth, and reproduction (12). Some hair is ingested along with meat, which may aid in faster passage through the intestinal tract. The degree of carcass utilization depends on variables such as prey vulnerability, carcass location, pack size, and time since last feeding (27). Wolves are adapted to a feast-or-famine diet and can overcome periods without fresh carcasses through food caching, reduced activity, and scavenging old prey carcasses.

Paramount to understanding the role of wolves in ecosystem function and structure is the knowledge of their foraging ecology. Studying the long-term predator-prey relations of a restored wolf population in YNP will not only increase our understanding of ecosystem function, but will be important for managers involved with wolf and ungulate issues in the GYE (14). Many of the patterns on wolf predation and feeding behavior reported here agree with other studies [see (29) for review]. We predict that patterns of predation and feeding behavior will change as a response to variations in biotic and abiotic factors such as prey density, vulnerability, wolf density, and weather.

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