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One of the best known facts about wolves is that they kill hoofed animals (ungulates) for a living. In North America, these include everything from deer and mountain goats, to bison and muskoxen. Less understood is how wolves kill these animals. This may seem trivial, but misconceptions about wolf hunting behavior are a key source of the misunderstanding and mythology about wolves. Beneath many debates about wolves is a fundamental confusion about the ability of wolves to kill ungulates.

The root of this confusion is the presumption that wolves are outstanding hunters. This is an understandable view. Few other mammalian predators can kill prey so much larger than themselves. Wolves also hunt in packs, and there are few spectacles in nature as impressive as a swarm of wolves chasing and taking down a large ungulate. People may have a special appreciation for this because not long ago most humans also made their living by cooperatively hunting big game. The key difference, of course, is that humans hunted with tools. The spectacular ability of wolves to cooperatively kill ungulates several times their size with only their teeth as weapons often elevates them to a place in the human imagination reserved for powerful natural and supernatural forces, such as tornadoes and Moby Dick.

Human imagination has played a big role in popular (mis)understanding of wolf hunting behavior because direct sightings of wolves chasing and killing prey have been rare. Most wolves inhabit areas too densely forested or too remote to allow regular observation of their hunting behavior. As a result, general knowledge about wolf hunting behavior has been heavily influenced by hearsay, nonobjective accounts, and interpretations of tracks in snow. Although Murie (1944) compiled the first scientific observations of wolf hunting behavior, this remained a murky area of science until the stud-

ies of Isle Royale wolves by Mech (1966) and Peterson (1977). These researchers pioneered the technique of using small fixed-wing aircraft to observe wolves from the air. This allowed the researchers to witness and record an unprecedented number of wolf-prey interactions, all of them involving moose, the only ungulate on the island. Their surprising finding was that most moose escaped unscathed, even when cornered by more than a dozen wolves. Subsequent observations of wolves hunting Dall sheep (Haber 1977, Mech et al. 1998), muskoxen (Gray 1983), bison (Carbyn et al. 1993), white-tailed deer (Nelson and Mech, 1993), and caribou (Mech et al. 1998) confirmed that most wolf predation attempts usually fail.

Why are wolves so often unsuccessful in catching their prey? Although the outcome of any species interaction is contingent on the traits of each species, traditional explanations about the low success rate of wolves have mainly focused on the role of prey traits. The central hypothesis has been that wolf-killed prey "must be disadvantaged in some way, for they would have escaped if they were not" (Mech 1970). Because aerial observations often provide only coarse details about wolf-prey interactions, researchers have used the remains of kills to infer how prey traits affect wolf hunting success. By comparing the traits of wolf kills to those of animals killed for other reasons (e.g., hunters, vehicle collisions), researchers have shown that wolves primarily kill young, old, and debilitated animals, which comprise a small fraction of the total prey population (reviewed by Mech and Peterson 2003). The conclusion from this research is that wolves are often unsuccessful because most prey populations are dominated by individuals they cannot catch.

But why can't wolves catch these individuals? To answer this question, one must appreciate how the traits of wolves constrain their ability to kill. The most obvious trait is skeletal. In general, wolves lack a specialized skeleton for killing. Its front-most teeth, the incisors and canines, are their only tools for grabbing and subduing prey; and these wear out with age (Gipson et al. 2000). Also its skull is not mechanically configured to deliver a killing bite like some other mammalian carnivores, such as felids and hyaenids. Specifically, a relatively long snout reduces the force of jaw-closing muscles that is exerted at the canine tips during the bite (Wang and Tedford 2008). In addition, the joint where the jaw connects to the skull does not allow the jaw to be locked or heavily stabilized when biting prey (Peterson and Ciucci 2003). Wolves also lack retractile claws and supinating, muscular forelimbs, which precludes them from grappling prey as do other large carnivores (e.g., cougars, grizzly bears).

Less obvious traits, including age, body size, and social behavior, can further limit wolf hunting ability. This information derives from observations of wolves hunting elk in northern Yellowstone National Park. This research differed from past efforts because it was based on the behavior of individually-identifiable wolves with known life histories. These animals were either members or descendants of the population reintroduced to Yellowstone in 1995-1997 (Bangs and Fritts 1996). Observers could measure the hunting behavior of individual wolves because (1) many were radio-collared and/or had distinct features (e.g., pelage markings, color, body size and shape), and (2) it was possible to watch wolves for extended periods from fixed positions on the ground, often from overlooks that afforded a bird's-eye view without the tight-circling and fuel restrictions of a fixed-wing aircraft. Ground observations provided extra time to carefully dissect the identities and roles of different pack members, as well as to record the entire sequence of a wolf-prey interaction from start to finish (MacNulty et al. 2007). Ground observations were made possible by northern Yellowstone's sparse vegetation and year-round road access.

Yellowstone research showed that the hunting ability of wolves, like the escape ability of their ungulate prey, decreases with age due to physiological senescence (MacNulty et al. 2009a). Top-performing hunters were 2-3-years-old. This highlights how age-specific change in hunting ability transcends differences between pups and adults to include differences between adults and old adults. Moreover, decline of hunting success with age suggests that temporal fluctuations in the age composition of the wolf population might contribute to the impact of wolf predation on elk numbers. And among wolves of the same age, smaller ones were generally worse hunters than larger ones because absent specialized killing morphology, sheer mass was necessary to topple an adult elk that is 2-6 times larger (MacNulty et al. 2009b). Indeed, male wolves were better than females at dragging down elk precisely because they were heavier. On the other hand, a lighter build may have given females an advantage when sprinting after fleet-footed elk.

Analyses of the effect of pack size on the success of wolves hunting elk revealed that group hunting behavior did little to offset age-and size-specific constraints on individual hunting ability (MacNulty et al. 2012). Packs with four wolves were more successful than packs with fewer wolves; but in packs with more than four wolves, pack size had no measurable effect on the outcome of wolf-elk interactions. Results suggest this was due to wolves holding back (i.e., free riding) to avoid injuries which arise from being kicked, trampled, or stabbed with antlers. This pattern held regardless of whether a wolf was a pup or an adult and suggests wolves in large packs may join a hunt simply to be at hand when a kill is made.

By contrast, the success of wolves hunting bison increased across pack sizes over which elk capture success was constant (4-11 wolves) and leveled off at a group size over 3 times larger than that of wolves hunting elk (13 wolves; MacNulty et al. 2014). Wolves were probably more cooperative hunting bison than elk because a single wolf has practically no chance of killing an adult bison by itself; whereas, a single wolf has about a 2% chance of killing an adult elk by itself. Low solo capture success is expected to foster cooperation because it leaves ample scope for an additional hunter to improve the outcome enough to outweigh its costs of active participation (Packer and Ruttan 1988).

The bottom-line is that the wolf's own biology enforces strict limits on its capacity to kill ungulates. It is precisely these limits that prevent the wolf from behaving as a runaway killing machine (Mech et al. 2015). Nevertheless, proponents for and against wolves rarely begin their arguments with a recognition of what wolves cannot do. Instead, both sides typically exaggerate the predatory power of wolves to advance their respective views about the ecological virtues and vices of wolves. Bridging the gap between these two views requires a shared understanding of the limits of wolf hunting ability.

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