HUMANS AND HOWLS:

WOLVES AND THE FUTURE OF ANIMAL COMMUNICATION

by

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ABSTRACT

Wolf howls have seldom been subjected to studies focusing on their semantic content, especially in wild populations where the context is natural but the availability of contextual clues for researchers is limited. The meaning of wolf howls as interpreted by humans depends on the human's position in ecological, cultural, and scientific context. I describe human interpretations of wolf howling from the perspective of amateur observers, historians, and biologists; the historical context of wolf howl research within ethology and questions about semantics in animal communication research; and the possibility of semantic differences in wolf howls from different contexts recorded in the wild. Wolf howls were recorded in Yellowstone National Park in 2017 and howls from territorial borders were compared with howls from territory interiors. Howls from the two groups were not discriminable. There may be no structural differences containing semantic information about territorial content, or the location relative to a border may not be a useful proxy for territorial message. Questions about intended meaning as opposed to observed function in animal communication are difficult to answer and often collide with humans' desire to be unique in their communication systems. Questions about wolves run into political and cultural baggage arising from humans' and wolves' history as ecological competitors. As semantic research in animal communication develops, wolves may become a coveted subject species because of their social living, strong individual/personal characters, and group coordination. These studies and their results will always be filtered through a thick barrier of human biases and reflections—possibly more so than any other non-primate in the world—but information about wolf communication can be disentangled from human culture in both scientific and vernacular accounts with enough historical information about the sources of the humans' biases. Future research on this topic will require simultaneous approaches from different angles, including ethological, historical, neurological, perceptual, and socioecological.

CHAPTER ONE

HUMANS STUDYING WOLVES

> *Yet it was an inexhaustible thrill to watch the wolves simply because they typify the wilderness so completely.*
>
> –Adolph Murie, 1944

When a human hears a wolf howl, they glimpse one aspect of a relationship between individual animals: someone howls and someone else hears and responds. Other relationships are evident in the same event. The presence of a wolf howl in the auditory landscape of a place indicates the presence of wolves in the environment, a presence defined by relationships between predator and prey, providers and scavengers, family and rivals. When the howl lands on the ear of a human observer, another set of relationships appears. The angles from which humans approach the howls of wolves depend on how they relate to concepts that change with time, politics, geography, and history. I will argue that the nature of wolf life, the content of wolf howls, and the relationships between wolves and humans can best be understood in the context of both wolf and human socioecology and cultural approaches.

Ethology came to North America in the 1940's, carrying the idea that animals and their behaviors could only be fully understood in their evolutionary environments and a call for students of animal behavior to step out of the laboratory and pick up their binoculars. In the mid-2000's, historians began to look at nonhuman animals as actors and attempt to include their ecology, social dynamics, and motivations in the stories of events that hinged on human-animal relations. The methodology required for the study of wolf communication and the way humans

have interpreted it over time will require historians to engage in ethological observation in order to understand wolves as historical actors; it will also require wolf biologists to bring humanist methods into their ethology in order to understand wolves as cultural beings.

This chapter will lay out the historical background of wolf-human relations in North America, primarily in the western United States and Yellowstone National Park. Like phenotypes and genotypes, cultural concepts influence actions that in turn change the environment in which those concepts are evolving. Research on wolves and their howls must be contextualized in terms of humans' concepts of wolves and their ecology, and the state of wolf ecology in turn is contextualized in a history of human actions tied to concepts of their relationship to wilderness and predators.

The first section follows the American war on wolves and traces the concepts that influenced it and emerged from it. These concepts shaped humans' understanding of their own place in nature, their goals and responsibilities with respect to wildlife, ideas about which wild animal species count as wildlife, the purposes of conservation, the value and vulnerability of species, and the nature of relationships between species in an ecological community. The second section looks at topics and players in early wolf research in North America, the continuities between the early research and ongoing long-term wolf projects, the relationships between wolf studies and conservation efforts, and the factors affecting what kinds of questions humans ask about wolves in different places and times. The final section summarizes how this all applies to Yellowstone and how its history and national park status interact with concepts and approaches in wolf conservation and research.

Prior to the 1930's, cultural and political barriers to the scientific study of wolf ecology and behavior in North America— including the near-extirpation of wolves from the continental United States due to federal eradication programs— largely prevented wolves from being present during the development of fields like ethology and bioacoustics. Those disciplines with their particular paradigms and methods were fully formed before American biologists began to apply them to wolves in the wild.

Captive studies provide easy access to information on genetics, physiology, and genealogy as well as an opportunity to observe behaviors closely and describe them exactly. The drawback is that they often fail to capture the full range of normal behavior and the evolutionary significance of behaviors without the normal context. Field studies are usually focused on ecological questions about population dynamics, predator-prey relationships, and how wolves interact with humans and human activities such as animal agriculture; they often center on specific populations in remote or protected areas like national parks, national forests, and wilderness areas. When behavior is studied in the field, although more difficult to observe, it reveals social and evolutionary information that was unavailable in captivity. Wolf studies in North America rarely, if ever, pioneer new methods. It could be that the controversial nature of wolves as a topic precludes them from being a model organism in trailblazing studies. Humans consistently argue about wolves, so they may not be likely to accept conclusions from wolf studies (especially if they have implications for management decisions) unless they come from accepted, blackboxed methods (Latour 1987).

European settlers in North America viewed wolves with suspicion and fear. Mentions of wolves in colonial letters and diaries describe them as cowardly, murderers, thieves, and outlaws

and their howls as “dismal noise” and “altogether doleful” (Coleman 2004, 163; Lopez 1978, 175). Biological or natural-history interest in wolves was rare apart from specific questions about how to kill them more effectively. The American war on wolves, along with similar efforts throughout Europe and other regions that preceded or emulated the American extermination campaign, was largely responsible for the late start to basic ecological studies of wolves in the wild. It also created cultural images of wolves that survived long after the war and continued to influence human interpretations of wolf behavior and vocalizations. The final stages of the war on wolves and the beginning of serious wolf research in America coincided with the end of World War II and the spread of ethology from Europe to North America, but wild wolf populations were depleted after the wolf war and their need for human-assisted recovery efforts in those years kept wolf researchers focused on population numbers and predator-prey ecology rather than social and behavioral questions.

The American War on Wolves and Perceptions of Wilderness

From the beginning of European-influenced agriculture in America and continuing into the present, humans have viewed wolves as a symbol or representative of wilderness. Whatever the prevailing public opinion on wilderness happens to be, such is the opinion on wolves. During colonization wilderness was the explicit enemy of mankind, something to be continually defeated on the frontiers to make room for civilization, and wolves were not only ecological competitors incompatible with the colonists’ desired form of animal agriculture but representatives of the uncivilized landscape. During the rise of modernity wilderness was a sad but necessary casualty of the march of human progress, and wolves were heroic but doomed figures of a bygone era to be preserved only in those places where they did not interfere with

human activity. People like Enos Mills and John Muir advocated for preservationist approaches to wilderness in the early 1890's, but these attitudes did not become mainstream until later in the decade. Even then, moves to conserve wilderness were mostly based in utilitarian reasoning. The intrinsic value of wilderness was recognized and melded with its aesthetic and cultural value, but it did not always include large predators. The rise of ecological thinking in the next century led humans to value wolves for their role in ecosystems, for the sake of biodiversity as both a utilitarian and an aesthetic goal, and as an indicator of the health or "wildness" of a landscape. Thinking about individuals, social groups, and subjective experiences eventually led humans to acknowledge the intrinsic value of wolves for their own sake, although in the realm of management, wolves are viewed primarily through an ecological spotting scope.

In colonial America, wolves were often killed by hunters and trappers. State and regional bounties beginning in 1630 provided extra incentive for the killing of wolves, citing their destructiveness to livestock. Colonial wolf bounties were usually paid in cash by the town, city, or colony where the wolf was killed; but some (often Indian-specific bounties) were paid in materials such as corn, tobacco, cloth, gunpowder, ammunition, and hunting rights. Some colonies included tributary laws with their wolf bounty laws—in 1668, Virginia required tribes to pay tributes in wolf heads (Hening 1823 cited in McIntyre 1995).

Bounties drove poisoning in the late 19th century. Poison is indiscriminate and killed domestic dogs as well as wolves. Rancher-photographer Evelyn Cameron relied on dogs for hunting and several dogs are named in her diaries (including one who died of poison), but she seemed nonchalant about dogs being caught in the crossfire of the wolf wars: "All sheepmen get their dogs poisoned, the bounty of $3.00 having made wolfers put poison everywhere" (Cameron

1895). An account from W. E. “Limestone” Wilson of a buffalo hunt in the 1880’s mentions a dog who died after eating from a strychnine-laced antelope carcass apparently set out for wolves (Wilson 1880). Both Wilson and Cameron attempted a remedy involving melted lard, and then seemed to take the poisoning as a fact of life. Contrast this with an observation of Granville Stuart, one of the earliest Montana ranchers: “Every tribe of Indians… was the avowed enemy of the wolfer as they lost many of their dogs from eating of the poison bait” (Stuart 1866-67).

Although wolfers from the 1850’s to 1880’s killed the most wolves for their pelts using poisoned carcasses (McIntyre 1995, 53), the bounty system backed by livestock owners continued throughout the west into the 19th century. In 1899, cattleman AJ Bothwell proposed a west-wide bounty system to make “the warfare against wolves” effective, until “the race is finally and completely exterminated”. New Mexico rancher Arthur Tisdale had first suggested a federal role in wolf extermination in 1897 (Robinson 2005, 47-48). Western ranchers were dealing with an arid landscape in which more land was needed to sustain each animal, so they were resistant to the idea of land reserves from which livestock could be banned, even when the bans were unenforceable. The US Forest Service was formed in response to concerns about uncontrolled deforestation, and from the beginning there were tensions between the move to conserve forests (mainly for utilitarian reasons along the lines of “wise use”, although the rare Enos Mills or John Muir supported preserving wilderness for its intrinsic value) and the western aversion to restrictions on homesteading, timber cutting, and livestock grazing. The USFS later initiated federal wolf extermination as a move to draw support for their conservation programs in the face of resistance from ranchers who wanted free use of public land for livestock grazing (Robinson 2005, 49-52). New agencies must actively recruit support before they can be taken as

established authorities, and the was on wolves was initiated as part of the USFS's recruitment when it found itself in a conflict between two concepts of how humans should relate to natural resources: conservation and free use.

In 1901, Teddy Roosevelt appointed Gifford Pinchot as conservation adviser. Pinchot, knowing that the Department of the Interior was controlled by the National Livestock Association, transferred the Forest Reserves to the Department of Agriculture in order to instate grazing permits on USFS land. Ranchers complained that they should not have to pay a fee to graze on land with wolves and other predators—unless the Forest Service would provide protection from the predators. So, in 1905, the Forest Service (with the help of the US Biological Survey[1] and the rest of the Department of Agriculture) started to pay for the trapping and killing of wolves on the reserves, first buying traps for use by rangers and then hiring hunters and trappers (Robinson 2005, 53-55). In the same year, Montana passed a law requiring the State Veterinarian to capture wolves and coyotes from eight counties, infect them with mange, and release them back into the wild (MT H.B. 251: An Act to Provide for the Extermination of Wolves and Coyotes, 1905).

The 1910's saw a budding realization that wildlife species were under threat, but the source of the threat and the nature of the required management actions remained obscure. There was also a question of "who counts as wildlife?" and the answer in early 20th century

[1] Also known as the Division of Economic Ornithology and Mammalogy (pre-1896), the Division of Biological Survey (1896-1905), and the Bureau of Biological Survey (1905-1940); in 1940 it was combined with the Bureau of Fisheries to create the US Fish and Wildlife Service.

conservation was not “all wild animals” but excluded large predators as a matter of course. William T. Hornaday’s 1914 statements on wolves in *Wild Life Conservation in Theory and Practice* demonstrated a popular angle of conservation at the time: utilitarian and herbivore-centric. Hornaday was a zoologist and taxidermist who campaigned for national forests to be made into game preserves (“with all hunting forever prohibited, save of predatory animals”) after being horrified by the extinction of species. He founded the American Bison Society in 1905 to facilitate the reintroduction of bison after they had been extirpated in part by scientists and collectors wanting to kill them for specimens before they were totally extinct (Robinson 2005, 93)—humans were grappling with the threat of extinction, but only as it pertained to them: bison going extinct would be bad for humans because they would miss out on collecting and studying specimens, but they were not as concerned about extinction being bad for the bison themselves (much less bad for their predators or grassland maintenance). Still, he described predators not as species but as a danger to the species worth preserving: “At the head of this list of evil-doers stands the big Gray Wolf or Timber Wolf, strong of limb and jaw, insatiable in appetite, a master of cunning and the acme of cruelty… Ever since the range steer took the place of the American bison, a relentless warfare has been waged against the gray wolf.” Hornaday then explains that wolves have already been “reduced to scattered fragments”, much like the bison he lamented, but concludes with “Wherever found, the proper course with a wild gray wolf is to kill it as quickly as possible” (Hornaday 1914, 140-142).

There was fairly unanimous acknowledgement in writings from the 1800’s onward that the conflict between humans and wolves was caused by humans eliminating bison and replacing them with cattle, but this was seen as inevitable and not in need of justification or rectification.

Bison-killing was not only for the fur trade but also a war tactic: General Philip Sheridan went to the Texas Senate and House joint assembly in 1875 as they were discussing a bison protection bill and said "[bison hunters] have done more in the last two years and will do more in the next year, to settle the vexed Indian question, than the entire regular army has done in the last 30 years. They are destroying the Indians' commissary… let them kill, skin, and sell until the buffaloes are exterminated. Then your prairies can be covered with speckled cattle, and the festive cowboy, who follows the hunter as the second forerunner of advanced civilization." Hunter John R. Cook, who related Sheridan's speech in his 1907 book *The Border and the Buffalo*, noted that if he had been "a child of this wonderfully prolific game region" he would have had the rights of occupancy and not "some outside interloper", but he quickly dismisses questions of rights as "sentiment" and invokes a popular 19th century misinterpretation of evolutionary theory: "it is simply a case of the survival of the fittest" (Cook, 1907). The wolf war was an extension of this tactic and ideology: wolves were here first, but whoever can kill them inherently deserves to replace them.

Interestingly, the same colonialist narrative with parallel roles for wolves and aboriginal humans played out in Hokkaido before and during the Meiji Revolution. In the 18th and 19th centuries, the Japanese saw a dichotomy between the inside world and outside or other world (agricultural lowlands vs. mountain wilderness); the outside was considered sacred but also uncivilized and anxiety-producing. The Ainu, who had only small-scale agriculture as a supplement to hunting and gathering, saw the world as a unified whole with no sharp distinction between inside and outside. Wild mountains and the wolves that inhabited them were sacred but not separate or intimidating (Walker 2005, 94). A similar difference in perception existed

between European colonists and Plains Indians in North America; one world with wolves as a part of it vs. separate worlds of civilization and wilderness. In both places, wolves grew to symbolize wildness and barriers to colonization. The Meiji government supported ranching operations as part of the colonization of Hokkaido. Forced assimilation of the Ainu in the early 19th century led many to become professional deer hunters as they were unable to hunt and fish normally; like the slaughter of bison in North America, this put pressure on wolves and feral dogs as their prey base was killed off and then replaced with livestock. In some places Ainu hunting dogs were blamed for killing foals, and government dog killers were sent to hunt them down. Ainu were made to kill wolves as a sign of fealty to the Meiji order just as Native Americans in Rhode Island were forced to pay tribute in wolf pelts (Walker 2004, 130-169). The Japanese wolf extermination later mirrored the American campaign exactly, even importing American wolf-killing experts to defend Hokkaido's new horse ranches against wolves. European wolf-extermination events (based in ecological competition over animal agriculture, particularly sheep) did not usually occur in the midst of colonization, so no particular group of humans was assigned to a wolf-parallel role like the Ainu and various Native American groups, but many European groups used wolf imagery to refer to their enemies in wars (Coleman 2004).

Ten years after the Department of Agriculture began funding wolf trapping on some public land, the Biological Survey was granted $125,000 "to be used on the national forests and the public domain in "destroying wolves, coyotes, and other animals injurious to agriculture and animal husbandry" (Agriculture Appropriation Bill, 1916), for a total federal budget of $281,190 (Robinson 2004, 195). In the same year, the Survey began replacing its top officials with non-

biologists, and by 1930 only one biologist remained in an executive position and the agency viewed researchers as a nuisance (Howell 1930). This completed the Survey's shift from a research agency that focused on the economic aspects of ornithology and mammalogy to one whose purpose was the systematic destruction of predators throughout the country. It was well-known that only a small percentage of wolves killed livestock, and by 1919 complaints of wolf depredation were few, but agencies desperate for congressional appropriations nonetheless decided to aim for "absolute extermination" (J. Stokley Ligon of the US Biological Survey cited in McIntyre 1995, 17-18).

The 1916 appropriation launched the most organized institutional extermination campaign against wolves and other predators. Propaganda pushed by Stanley Young and others led states, counties, and stockgrowers' associations to contribute funds to the Survey for predator and rodent control which almost matched federal appropriations, which quadrupled from 1915 to 1928. By then, wolves had already been defeated. The number of wolves killed by the Survey in Colorado had declined to one per year by 1925 (Robinson 2005, 188). In 1928, only 11 wolves were killed by federal hunters throughout the country—compared to over 80,000 coyotes including the Survey's estimate of coyotes poisoned but not recovered (Redington 1928). The last few wolves in the country were killed in the 30's and 40's; by 1944, Young wrote in *The Wolves of North America* that "little wolf control work is now justified" and that in the places where they still lived (such as Minnesota's Boundary Waters where the network of lakes prevents livestock grazing) they "may be allowed to continue their existence with little molestation" (Robinson 2005, 286).

The war on wolves ended for three interconnected reasons. The first was that the government simply ran out of wolves to kill. Federal employees whose jobs depended on getting rid of wolves were faced with the fact that completing their jobs meant losing funding for their departments and putting themselves out of work. As the number of wolves in the contiguous 48 dwindled, the Biological Survey tried to redirect its extermination campaign toward other animals. When the Survey had largely eliminated wolves, they used coyotes as an excuse to maintain their excessive budget; the small canids flourishing in the empty niches left by absent wolves were now "the most destructive beast that roams the home of our game"[2]. Although coyote populations were more resilient than wolves, in part because of their greater fecundity and flexible social structures (Flores 2016), by the 1930's even they were in danger from indiscriminate poisoning of themselves and their prey. Olaus J. Murie wrote in 1952 that "In extensive areas, many who had formerly taken for granted the presence of Señor Coyote and his song, without much thought, now miss him, now that he is gone." Although they did not need a large ungulate prey base like wolves and were better able to thrive in human environments, coyotes were extirpated in some areas while poisoning campaigns were waged all across North America. Some park service correspondence referenced coyotes being "all but exterminated" in areas with runaway deer populations in need of predation in the early 1950's, when federal poisoners encircled parks with poison baits and occasionally snuck illegal poison inside park

[2] While Utah settlers, eager to wrap up the conquest of the wild by being rid of wolves, turned "prairie wolves" into coyotes (Coleman 2004), the Biological Survey desperate for self-preservation turned coyotes into surrogate wolves.

borders. Regardless, the national parks served as sanctuaries for coyotes and may have been instrumental in preventing their extinction (Robinson 2005, 299-300). Young began "a campaign against magpies" in 1926 because they took the baits meant to poison coyotes, indiscriminately poisoning scavengers of all kinds; rodents also became a target after many of their predators were killed off by the Survey (Robinson 2005, 169-171). Despite claiming a scientific basis for their actions, the Survey followed a train of predictable problems of their own creation as they chased federal appropriations, and their veneer of credibility soon fell away.

The next reason for the end of the wolf war was partly a product of their decline. Public perception of the character of wolves largely depended on media representations, which shifted away from using wolves as boogeymen toward the end of the wolf war. This shift began with a nostalgia that was only possible because the wolves appeared to be doomed to extinction, as Jon Coleman describes in *Vicious* (2004). The beginning of this nostalgia was the rise of the "last wolf" narrative. Toward the end of the war on wolves, the remaining wolves in the continuous 48 states were often loners whose packmates had already been killed or members of a single pair rather than a complex pack, as is characteristic of disrupted populations (Smith & Ferguson 2005, 93). Many had unique and recognizable footprints because they had already encountered and escaped traps, losing toes or entire feet in the process. All this made for a group of last wolves that could be made famous, idolized, romanticized, and nevertheless killed for the sake of modernity.

European-American perceptions of wilderness, wolves, and Native Americans followed parallel trajectories from scary (antagonists of the colonizing Europeans, "savages", "outlaws[3]", threats to civilization that must be destroyed) to melancholy (doomed "last wolves", "noble savages", dying wilderness; all with the assertion that their demise was sad but necessary for the progress of "civilization") to nostalgic (used in stories to symbolize the colonial past, to represent hardships endured for the sake of building civilization, and to mourn the loss of the "man against wild" pioneering narrative on the 19th century frontier; also represented things like wildness, innocence, and freedom). Once the extinction of their enemy was deemed inevitable, only then did the European-Americans project positive traits onto them—but "positive" should not be mistaken for "realistic"[4]. Last-wolf narratives fully embraced the noble savage archetype and filled their wolves' heads with human-like internal monologues filled with resignation and acceptance that modernity must rise and therefore wolves must die. Stanley Young and Arthur Carhart wrote several typical last-wolf stories in *Last Stand of the Pack*, but by the time it was published in 1929 they were already going out of fashion. The public was less interested in accounts of humans killing wolves, even noble ones; they now wanted stories where the wolf wins. Young and Carhart's vignettes resembled earlier last-wolf stories like the 1898 story

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[3] A shift in the American wolf image from cunning, sly, cowardly thieves to ferocious murderers, killers, and criminals has been documented in both the eastern and western US. Michael Robinson credits Stanley Young with harnessing cultural reactions to the rise in violent crime during the Prohibition era to begin the shift. Along with the increasing scarcity of wolves and resulting tendency to dramatize accounts of the remaining ones, this made words like 'killer' and 'murderer' ubiquitous in media reporting on wolves after 1921 (Robinson 2005, 153).

[4] Coleman (2004) argues that the success of wolf recovery did not rely on ecological facts as much as the cultural shift in attitudes toward wolves that grew out of the last-wolf trope; sympathetic doomed wolf characters made the general public willing to put time and money into reintroduction and recovery efforts.

"Lobo, the King of Currumpaw" by Ernest Thompson Seton, from whom Young borrowed many of the last-wolf tropes and narrative conventions (Coleman 2004, 208-210). But while Seton ends with the moral that "each of our native wild creatures is in itself a precious heritage that we have no right to destroy", Young clung to the Survey line that "the grey wolf has no place in modern civilization" and so wolves had to be destroyed to enable humans to achieve their destiny of living in the American West, even after most biologists and members of the public, including his co-author Carhart, ceased to believe that wolves should be exterminated just "to please squawking stockmen" (Robinson 2005, 222-223). Even when the doomed wolves were portrayed as heroic or noble, last-wolf stories emphasized their fearsomeness and decried them as dangerous killers. These tales accepted sheep and cattle ranchers' exaggerations without question, so that the outlaw wolves were blamed for killing more livestock than a wolf could possibly kill in one lifetime (Gipson 1995).

Three decades after *Last Stand*, another kind of wolf appeared in popular media when Farley Mowat published the infamous *Never Cry Wolf* (1963). This book was intended as an antithesis to anti-wolf propaganda. Mowat called it "deliberately unscientific", aiming to sway public opinion in favor of wolves while taking the same kinds of literary license to emphasize their moral and honorable attributes as the anti-wolf propaganda did to frame their depredations as burglary and murder. It was no more factual than Young's stories, and scientists despised it. Biologists were uncomfortable with the idea of using misinformation to foster a desire to protect wolves, believing that a public interested in saving a fictionalized species would lose interest after discovering that real wolves exist on their own terms instead of fitting perfectly into a human literary archetype. Mowat's strategy was effective—*Never Cry Wolf* instilled a bias in

favor of wolf conservation in popular culture that lasted into the 1990's—but managers continued to see misinformation that came from Mowat (such as the belief that wolves preferentially eat small rodents) in the public (Jones 2003, Grooms 2008).

Regardless, a major factor in public concern for wolf conservation was the propagation of stories and images designed to foster empathy. An earlier example demonstrates how the shift toward sympathetic depictions of wolves intersected with the beginning of an ecological turn in conservation thinking, as The Emergency Conservation Committee in the 1930's struck a balance more palatable to scientists than Mowat's direct aim at public opinion that bypassed ecology. The ECC was a small organization[5] that published pamphlets explaining ecological issues and corruption within relevant organizations with a focus on ending the USBS control program. The pamphlets contained no information that was not already available to the public, but they presented the information concisely and were calculated to keep attention on the issue. While the mammalogists were "carefully moderate" and many were gentle in their criticisms of the Survey because they remembered a time when it was truly a scientific agency, the ECC was willing to use dramatic, attention-grabbing language (Robinson 2005, 252-253). Like Mowat in the 60's (and Leopold in the 40's), they knew they needed to play on the public's emotions, but unlike Mowat they stuck to the facts and unlike Leopold they stuck to ecological motives instead

[5] Rosalie Edge, an amateur ornithologist famous for founding Hawk Mountain Sanctuary in 1934, started the ECC in 1929 after discovering that naturalists and journalists were being prevented from publishing on the USBS's poisoning programs due to USBS influence on publishing houses and involvement in a "small wildlife clique" that included the Audubon Society and the American Museum (Robinson 2005, 247-249).

of calling for people to support wilderness because it might provide cultural, spiritual, or recreational benefits to humans.

The appearance of the sympathetic wolf character in human culture coincided with a shift in how the humans thought about and interacted with wilderness. Nostalgia for wolves was only one facet of a wider nostalgia for wilderness, both for its own sake and for lost human lifestyles: people mourned the struggle against wilderness and then the wilderness itself. Nostalgia for the fight against wilderness appears in *Last Stand of the Pack* when wolf hunters express the melancholy recognition that their lifestyle is dying out along with the wolves. By that time, however, most Americans were experiencing nostalgia for the wilderness itself. Where Carhartt's trappers might think "I wish the wilderness was still here so I could keep fighting it", Americans after the taming of the West thought "I wish the wilderness was still here, and this time I would not destroy it". The dream of conquering the wilderness ended when there was hardly any more wilderness to conquer, and even with continued ecological competition between ranchers and wolves, the conflict grew distant for majority of Americans.

This was foreshadowed in the eastern US by comments like those in Henry David Thoreau's 1856 journal entry: "when I consider that the nobler animals have been exterminated here… I cannot help but feel as if I lived in a tamed, and, as it were, emasculated country" (Thoreau 1906, 220-221). He associated extinction with an undesirable tameness resulting in a degraded and incomplete landscape rather than a justified byproduct of the march toward civilization and modernity. As this tameness crept westward, Americans increasingly yearned for pristine, untamed, original wilderness—not only for wildlife but for themselves as an opportunity for recreation and expression of freedom and integrity of the land and its people.

Concepts about the value of landscapes shifted: where once a valuable land was defined by its usefulness to humans and a place like the Boundary Waters in Minnesota was considered worthless, now places with the least amount of human influence (by which they meant influence by white people), were valued for their closeness to some original state. Most of the American landscape was under extensive human influence before the arrival of European settlers, but 19th century writers popularized "the pristine myth" and the idea that native humans did not cause much change to the landscape (Denevan 1992). Native populations in North America declined by 74% between 1492 and 1620 (89% in the New World as a whole). Some effects of humans on forest composition in the east and grasslands in the Midwest were retained and absorbed into the settlers' idea of a pristine landscape, but this decline also allowed some of the humanized landscapes to return to a more "natural" state such that there was "much more 'forest primeval' in 1850 than in 1650" (Rostlund 1957 quoted in Denevan 1992). Even when Native Americans' changes to the landscape were noticed by settlers after the decline, there may have been a general understanding that their changes did not count as anthropogenic. Scientific racism placed nonwhite humans in a category between white humans and wild animals, whose alterations to the landscape are 'allowed' the way bison can maintain grasslands by literally trammeling the land, but as long as humans (particularly white humans) are not involved, that grassland is called "untrammeled". The parallel extermination campaigns against humans and wildlife, Indians and wolves, also reinforced the notion that the wilderness was whatever escaped the major effects of European colonization, regardless of other human activity.

Americans living on a tamed landscape now want to identify with wild animals, especially predators. Early Euro-Americans compared themselves to sheep to evoke images of an

innocent, peaceful, domestic flock besieged by their enemies, whom they compared to wolves and other wild predators. Present-day Americans have flipped these roles, even while they continue to cling to the power they have over nature. They surround themselves with images of predators that make them feel fierce and independent; they use the word “sheep” to refer to their enemies by comparing them to gullible, vulnerable prey. Colonists viewed civilization as power for humans as a species over the wilderness, but once the wilderness was conquered, “civilization” began to represent domestication taking power away from humans as individuals. The image of rugged individualism against society, free wolves against tame sheep, morphed with a romanticized image from the last-wolf days: the lone wolf. Humans in the American West don’t want to give up civilization’s power over the wilderness, but they resent the power that civilization has over them as individuals. The real wolf lives in the ‘wilderness’ and functions only as part of a social group. Americans live in ‘civilization’ but want to rebel against their social groups. They have taken the struggling survivor of a broken pack and turned it into a free, individualistic ‘lone wolf’. At the same time, they value the symbolic wolf for its loyalty to the pack, and flock to national parks to hear wolves howl and watch packs interact “in the wild”. Under all the contradictory symbols, places that are undisturbed enough to support wolves are “wild” enough to be valued for their aesthetic contribution to the human wilderness fantasy.

For many ranchers, however, wolves are still murderous creatures to be feared. Anxieties over federal control of land in the American West have been strategically redirected toward wolves by none other than the federal government itself. Federal wolf control no longer exists, but what remains is the psychological imprint of decades of USBS propaganda directed at politically powerful ranching and farming groups. As these groups grew less influential, the

Survey tried to appeal to hunters, saying that if wolves were not exterminated, there would be no wild ungulates left for humans to hunt. Vernon Bailey claimed in 1930 that wolves and game could not be maintained on the same range (Bailey 1930, 137).

While it should be clear that a predator that wipes out its entire prey base would never evolve in the first place (and if it did, it would have quickly gone extinct), it may be less obvious that wolves and human hunters have been living in North America for hundreds of thousands of years without intense conflict. Even where humans and wolves target the same prey species and are therefore competing for the same resource, humans from hunting cultures have not waged wars of extermination. Fritts et al (2003) suggest that widespread fear of wolves results from a genetic predisposition to fear predators, similar to the biologically prepared learning that may be responsible for the ease with which primates develop fear of snakes; but humans have never been a desirable prey animal for wolves, and the fear of wolves in humans is not universal. Hunting cultures without animal agriculture, such as the Blackfeet and Ainu, tend to admire wolves despite being ecological competitors. Where agriculturalists push out hunting cultures, they do the same to wolves, and agriculture-driven wolf killing campaigns spread negative views about the nature of the wolf.

The predator extermination efforts we have seen in Europe, America, and Japan all came from societies that increasingly relied on animal agriculture, which replaces wild prey on the land with domestic livestock (Walker 2005, 136). Attitudes about wolves can be traced to European agriculture, as European colonists imported their own imagined wolf packaged with an agricultural regime to North America, and Americans in turn brought the same package to Meiji Japan. Wolf killing and bounties in Europe often existed to defend sheep. Even proponents of the

wolf war in America knew to blame it on the replacement of bison by cattle on the plains. Horse ranching in Japan was one of the Meiji government's modernization tactics, complete with an imported wolf war that was at odds with the historical relationships between wolves and humans focused on plant agriculture. At Misakubo, Shizuoka, where people once worshiped wolves and asked them to protect their crops, they now resort to setting off timed explosions to keep herbivores away (Walker 2005, 73). While many authors attempt to place the origin of cultural wolf-hatred in folktales and religious fables, these stories could not have been imbued with an attitude that did not already exist. "Even without knowing stories such as "Little Red Riding Hood" or worshipping at Christian churches, traditions often targeted as sources of wolf hatred, Meiji officials saw the wolf as a "noxious animal" because the bottom line of industrial ranching demanded that they do so" (Walker 2005, 133). The story of "Little Red Riding Hood" could not have been created unless its intended audience already believed that wolves were dangerous. Fairy tales and religious symbolism almost certainly helped to spread the fear of wolves throughout Europe and then into colonial North America, but a vector for an attitude or bias should not be mistaken for its origin. There is a material reason behind the biases that made their way into these stories. The human societies with the most anti-wolf sentiment are agricultural societies with strong traditions of animal husbandry, especially industrial ranching (Walker 2005, 136). The result was the same in Japan as in Europe and North America: wolves were viewed as a necessary casualty of parallel socioeconomic processes (colonization and modernization) which were entangled with animal agriculture and ranching.

Humans who hunt but don't practice animal agriculture have historically respected and learned from the wolf as a hunter, a perspective that many American hunters lost or had taken

from them by the 1990's. Ideas about what it means to be a predator in human cultures are highly dependent on how those humans interact with their prey and whether they depend on hunting for survival or depend on animal agriculture with hunting as a supplemental source of food. Richard Baldes of the USFWS, whose son would later lead the reintroduction of bison to the Wind River Reservation in 2016, wrote an article on his perspective on wolf reintroduction as a Shoshone called "The Wolf as a Fellow Hunter":

> If there was ever a group of people that could have taken an adversarial role towards wolves, it was the Native Americans. They competed with the wolf directly for the same food supply—bison, elk, deer, antelope, caribou. Yet Native people chose not to destroy the wolf. They admired and respected the wolf for his mastery at hunting and survival and emulated his behavior (Baldes 1995).

Brenda Peterson noticed the manufactured nature of modern anti-wolf sentiment at the 1993 Wolf Summit in Fairbanks. Many hunters attending the summit expressed a hatred not explainable by simple ecological competition. Peterson believes "it is no longer human hunger that drives us to conquer and control and kill our brother predator as if he were our natural prey—it is a story of hate inherited from another century" (Peterson 1994).

While state propaganda was likely involved, Peterson also attributes this phenomenon to a hierarchal drive present in some modern hunting cultures. When it became popular for humans to view ecological relationships as a "food chain" that one could be at the "top" of, they began to view predation as a hierarchal competition, leading to the desire to wage war on wolves the way humans wage war on each other. Hierarchal conflict among humans was also involved. Inupiat villagers in 1993 told Rick McIntyre that the wolf control was "just a plan to make it easier for rich white people from Fairbanks and Anchorage to hunt" (McIntyre 1995, 461).

In 1995, Peter Steinhart described a decline in mutual respect in humans' predator-prey relationships. When hunting in the wild, they were more likely to see their prey as equals and

have a spiritual interpretation of hunting; but after the rise of animal agriculture, predation was less an exchange of energy from one autonomous animal to another and more an act of harvesting inert matter. Some believe there is spiritual value in meat that comes from a respectful hunt and that domestic prey animals like cattle 'don't have any spirit'. Spiritual or not, without a respectful approach to prey, humans became disconnected from the act of predation. Now it both fascinates them and disgusts them, and they do not know how to conceive of themselves as predators or how to think about other predator species (Steinhart 1995, 28-51). This cultural gap was filled in by conflicting impulses: a hierarchal drive (humans aiming for the top with the goal of controlling and harvesting everything else) and a moralistic one (the discomfort with death and killing when observing animals who must kill to survive was mobilized in favor of the humans' hierarchal aim in order to denigrate wolves as murderers).

From a resurfacing of the myth that ungulate populations would be wiped out by a native predator to crowds with angry picket signs to one beer-fueled comment saying that wolves have no souls, hunters at the Summit created the appearance of a large, threatening mob such that an onlooker would conclude that wolves were in serious danger from the majority of humans in Alaska. In reality, the hunts would have covered only 3.5% of the state (Steinhart 1995, 284), and only 8% of Alaskans supported state predator control. The governor and the Game Board, along with corrupt insider-only advisory boards, were pushing for "lethal management" on their own without input from the majority of Alaskans. After independent wolf researcher Gordon Haber released video of state officials killing wolves in traps, the next governor canceled the control program in 1995 because of public disapproval. To people who witness this "vehement anti-wolf sentiment", wolves appear vulnerable and in need of protection, even in parts of the

country where they are no longer endangered (Coleman 2004, 234), and what remains of the fear of wolves from the colonial and predator-control eras drives wolf protection.

The third element that took part in the end of the war on wolves and the beginning of restoration and reintroduction was an ecological turn in the thinking of researchers, policymakers, and the general public. There is an aesthetic change parallel to the beginning of ecological thinking which can be seen in wilderness nostalgia, where landscapes were valued for a sense of completeness or wholeness rather than for their utilitarian ecosystem functions. The aesthetic value placed on whole landscapes and wilderness intertwined with a growing ecological consciousness in the public and continues to be seated alongside ecology to this day, but the ecological turn itself revolved primarily around causes and effects, food webs and cascading effects of change, functions of systems, and ecosystem services.

The ecological concern with functionality included attention to some functions of predator niches which only came to light in the aftermath of the extirpation of wolves from the majority of the continental US. The role of predators in an ecosystem was overshadowed by early American ideas about managing land and wildlife in a pseudo-agricultural way, envisioning forests in which humans could eat all the large ungulates they wanted because there were no large predators. Landscapes were soon overrun with dense populations of sick and starving herbivores. From 1908 to 1920, elk populations fluctuated wildly. Populations boomed, stripped the vegetation, and then starved; increased density and lack of predators also caused the rapid spread of diseases. In Wyoming and Colorado, managers tried a multitude of different responses including feeding herds in winter, creating a national elk refuge, control and culling by

rangers, and sending elk away to parks and zoos, but nothing could stop the mass starvation. The winter of 1919-1920 cut Yellowstone's northern herd in half, bringing it from 25,000 individuals to 11,000 (Robinson 2005, 273). Without wolves, overpopulated elk destroyed aspens and willows, reducing the populations of beaver and bighorn sheep. 1930's poisoning campaigns also killed off rodents and birds, which allowed for a tick irruption that killed deer, cattle, and sheep as well as a grasshopper irruption that destroyed agricultural crops. Exposed soil caused by unstable herbivore populations and poorly managed cattle grazing combined with a drought in 1931, causing dust storms and eventually the massive dust bowls of 1934-5. Although Stanley Young was unrepentant and repeated Survey lines into the 1930's—denying that poison killed non-target animals and that livestock overgrazed national forests— people like Arthur Carhart and Survey founder C. Hart Merriam came out against the poisoning program (Robinson 2005, 224-252). Humans were forced to acknowledge that large predators were an indispensable part of ecosystem health and that their absence had effects that went beyond their immediate prey into the abiotic environment.

By 1920, most Americans were no longer intimately involved with ranching. Hunters still competed with wolves for wild game, but there was a decline in mass wolf-killing and anti-wolf sentiment born of paranoia over cattle and sheep depredation (Robinson 2005, 98). Investigations in the 1920's revealed that Survey poisoning campaigns caused loss of fur-bearing animals and that killing off predators caused rodent and deer irruptions. The Biological Survey tried to block the investigations, refused to reveal the number of poison baits they put out each year, and attempted to save its reputation by adding platitudes about "control, not extermination" to their 1924 annual report, and used the same vague language –intended to placate the public but allow

the Survey to continue extermination—at their 1928 conference. But after several years of official statements contradicting policy on the ground, which was still very much focused on extermination and continued to poison scavengers indiscriminately (Howell 1930), the mammalogists and the general public began to recognize the reality of the situation.

Until this point, disagreements between mammalogists and the BBS had been kept out of the public sphere. In 1930, A. Brazier Howell wrote the first public condemnation of the Survey by a mammologist: "it appears that the very existence of all carnivorous mammals, including those valuable species which constitute the chief check upon injurious rodents and are a vital element of our fauna, is imminently threatened over large areas. We therefore earnestly petition that this extensive program of poisoning operations be immediately abandoned". This petition was signed by 148 scientists and sent out to politicians, newspapers, and magazines. While Howell excluded large predators like wolves and mountain lions from his consideration, the Survey went on the defensive. (Robinson 2005, 212). 1930 was the first time the BBS's ten-year budget bill went to a hearing instead of being automatically approved. At the mammalogists' symposium of that year, Survey representatives introduced anti-coyote propaganda, calling the small canids "the archpredator of our time". This time, unlike in 1924, the scientists were willing to call out the Survey's dishonesty, noting the extreme political power of sheep men to exaggerate the damage done by coyotes and be allowed to overgraze all the land they wanted (Robinson 2005, 218-219).

Despite this consensus, the government (after 1940, the Fish and Wildlife Service) was slow to respond. Poisoning continued into the 1960's. An advisory committee including A. Starker Leopold came out with their investigation, known as the Leopold Report, in 1964; it

criticized the poisoning but gave no recommendations. By the time Congress halted poisoning following an investigation by the secretary of the interior (Rogers Morton, who announced the study with a claim that “performance will follow program so that our imperiled predators will not perish in a sea of platitudes”) leading to the Animal Damage Control Act of 1972, the FWS had almost eliminated the US populations of red wolves, black footed ferrets, and California condors; the last members of these species had to be taken into captive breeding programs in the 1970’s and 80’s under the Endangered Species Act (Robinson 2005, 307-320; Federal Animal Damage Control Act 1972, 31).

The 1960’s and 70’s were full of environmental protections, and the ESA in 1973 was reported as just another bill among many. Nixon’s speech introducing the Animal Damage Control Act in 1972 said “this is the environmental awakening”. Rachel Carson published *Silent Spring* in 1962, prompting humans to realize that they were not exempt from environmental issues that affected other species. Protection acts, exposes, and lawsuits led up to the ESA. Sheepmen and the Farm Bureau still wanted predator control in the late 60’s, and even in 1973 some sheepmen resorted to the moralistic language of colonists condemning predators as evil murderers, but by the 60’s predators were finally starting to come under the umbrella of general concern over extinction (Robinson 2005, 310-321). The ESA protected wolves during the late 70’s and 80’s when the government once again caved to the ranching industry, and recovery plans were made for wolves in the Northern Rockies and red wolves in the Southwest. Where conservation laws in the 1900’s were intended to manage resources for use by humans and viewed the country as tree farms and game preserves, the environmental legislation of the

1960's-70's had more ecological and preservationist goals along with the growing consensus that maintaining biodiversity was a worthy goal in its own right.

Aldo Leopold's essay "Thinking Like a Mountain" from *A Sand County Almanac* (1949) is widely considered a defining signpost of the ecological turn, but the shift was more gradual and less original than Leopold portrayed it. In "Thinking Like a Mountain", he describes an incident in 1909 when he and his crew shot into a pack of wolves because "In those days we had never heard of passing up a chance to kill a wolf" and killed one, possibly the alpha female; he relates how they reached the old wolf "in time to watch a fierce green fire dying in her eyes". "I realized then", Leopold says, "and have known ever since, that there was something new to me in those eyes—something known only to her and the mountain. I was young then, and full of trigger-itch; I thought that because fewer wolves meant more deer, that no wolves would mean hunters' paradise. But after seeing the green fire die, I sensed that neither the wolf nor the mountain agreed with such a view" (Leopold 1949). While Leopold's essays popularized the idea of a land ethic later in his life and after his death, his own conviction did not appear the moment he watched the green fire die. He did not have an instant ecological epiphany, but took decades of studying land health to develop his land ethic and take a position against predator extermination (Robinson 2005, 102; 273).

Leopold was preceded by several people who did have the sense of ecology that he lacked for most of his life. Sigurd Olson demonstrated a land ethic in the 1930's, when he undertook the first serious study of wolves on his own initiative, making his observations from snowshoes around Ely, MN. His paper concluded with a line that could have come out of

Leopold: “The timber wolf is an integral part of the wilderness community, the destruction of which would destroy the fine balance between related forms. To eliminate as vital a relationship as exists between predatory forms and the animals they prey upon, to destroy a mutual dependence, means that artificiality has entered the wilderness picture” (Olson 1938). John Muir and Enos Mills were preservationists in the early 1890’s, advocating for the intrinsic value of forests and wildlife; Mills emphasized observation and used his observations of predators to challenge assumptions about the destructiveness of wolves, bears, and cougars (Robinson 2005, 50; 102-103). Muir spent time in the field and saw nature as a whole due to his immersive experience. His work on establishing national forests and parks was aimed at protecting whole ecosystems at a time when it was more popular to think about “Resources Conservation and Development”. Because of Muir’s acceptance of the whole wilderness as “unity and interrelation” and his rejection of practical or utilitarian ecology aimed at manipulating nature for the benefit of human economies, Bill Devall (1982) called him a deep ecologist in reference to the ecological movement that began in the 1970’s; with his recognition that pieces of an ecosystem could not be taken apart, Muir was closer to a land ethic and thinking like a mountain a hundred years before Leopold achieved it.

Despite being late to his ecological awakening, Leopold has remained at the center of these conversations and influenced the way people talk about ecology and about wolves to this day. Barry Lopez (1978, 163) quotes trapper Lawrence Carson telling a story about killing a wolf that sounds very Leopoldian, even speculating about the opinions of mountains and focusing on the howl: “I wondered if the great mountains and deep silent valleys that had been his range would miss him. I wondered if at night, when the moon hung low like a great ball of fire, the

dark shaggy spruce trees would miss his wild, deep-throated call." Lopez is unclear about his sources throughout *Of Wolves and Men*; he implies that Carson was trapping in the 1930's but gives no indication of whether he gave his account before or after *A Sand County Almanac*.

Leopold either influenced or was anticipated by these kinds of "last wolf" stories in an aesthetic sense; in a land ethic sense he was preceded by earlier ecologically minded people but managed to capture the minds of readers and historians with "Thinking Like a Mountain". The essay pointed to ecological concepts that laymen were becoming conscious of in the 1940's: that states have extirpated wolves without realizing that in their absence humans must keep the herbivore populations down, that poor management turns droughts into dust bowls; and that while deer can be replenished in a few years, plant life cannot, so it takes a long time for a range to recover from too many grazers. It also provided a memorable snapshot that continues to stick in readers' minds and is quoted in every book or magazine article about wolf conservation: the hunter locking eyes with the wolf and watching the green fire dying in her eyes. Former Survey hunter Dick Randall and his son had their own "green fire" moment with a bobcat in 1973. After his young son saw "the light [go] out of its eyes", Randall was stuck by empathy for the bobcat and other predators he had been paid to kill. He quit the agency, released information about its law-breaking and allegiance to sheep farmers, and started campaigning against the control program (Robinson 2005, 325-326). "Once you've met the eyes of a wolf," said Blackfeet singer-songwriter Jack Gladstone, "they will never leave you" (McIntyre 1995, 338).

Besides human interests, population health, and ecosystem function, concern for individuals is another factor that drives conservation efforts. Leopold's use of eye contact in his

"green fire" story implies an individual empathy, but he never fully addresses it; he goes from that moment with an individual wolf to thinking about the ecological relationships of populations of predators, herbivores, and vegetation. By the end of his life, Leopold clearly respected predators for their utilitarian value to the land and ecosystem, but he was vague at best on predators as individuals. He stands in contrast to Muir, who valued wildlife as organisms and regarded individual animals as "fellow mortals and neighbors" (Muir quoted in Robinson 2005).

Rosalie Edge was the first person to introduce the issue of cruelty to individuals into the debate over the Biological Survey's control program; her background in amateur ornithology exempted her from pressures felt by mammalogists to avoid subjectivity and to go soft on the Survey because it was once a respectable scientific institution. One of Edge's ECC pamphlets from 1930 opposing the Survey's 10-year bill emphasized suffering when the mammalogists were unwilling to mention it (Robinson 2005, 205). Ecologist Jim Estes describes modern conservation coming from "populationists", who value the welfare of populations but not individuals. He suggests that management should take individuals into account "because the majority of our society has such a deep emotional attachment to the welfare of individual animals", implying that most individual humans find individual welfare important but that management for the conservation of populations often fails to reflect individual interests (Bekoff 2002, 188).

Concern for individuals rather than only for populations was always present in small doses, but not heavily influential in ending the war on wolves. Writers like Seton and Mowat used individuals to evoke sympathy in storytelling, but then carried readers around to a broader ecological message (Jones 2003). An Anti-Steel-Trap League formed in 1925, but its focus was

limited to one aspect of wolf killing; they never addressed poison or even whether wolves should be exterminated at all. In response to growing concerns in the 1920's regarding welfare, some propaganda claimed that strychnine killed quickly and painlessly—a statement believable only to those city-dwellers who had never seen the poison in action[6]; even notorious wolfer Ben Corbin, who killed pups in their dens by hiding fish hooks in pieces of meat, considered poison "unsafe, unfair, uncivilized" (McIntyre 1995, 125). Government hunter Albert K. Fisher reassured The Farm Journal readers that "to students of anthropology it is a well-known fact that savages and illiterate men suffer less from pain than those with high-strung mental development", and it follows that "lower forms of animal life" suffer less or even not at all from strychnine and steel traps (Robinson 2005, 159-160). This largely English version of the pre-Darwinian, hierarchal ladder of life (Bowler 1983, 300), with non-white "savages" on a lower rung than "civilized" Europeans (the presumed endpoint of the pre-determined course of evolution), reappeared whenever it was politically expedient to ignore one's ethical obligations to other humans or "lower animals", in this case six decades after *On the Origin of Species* (which turned the

[6] Ernest Thompson Seton wrote that he stopped using poison baits after seeing a coyote dying of strychnine and hearing a detailed firsthand account from 1893 of a human who drank strychnine after mistaking it for quinine and begged his companions to shoot him before he died. While this may be an exaggeration of his personal timeline (poetic license taken for the memoir just like Leopold's claim that he fell into a land ethic after that fateful hunt in 1909), his attentiveness to his moral obligations toward individuals was genuine at the time of writing: "What right, I asked, has man to inflict such horrible agony on fellow beings, merely because they do a little damage to his material interests? It is not right; it is horrible—horrible—hellish!" (Seton 1940, quoted in McIntyre 1995, 73).

diagram of life from a ladder to a tree) although still a little before the rise of Boasian anthropology (which ended the trend of arranging groups of humans on a similar ladder)[7].

Another factor, peripheral to ecological management but important in public perception, was the discussion of rights. Biologists and laypeople alike began to express the opinion that not only did individual wolves have the right to live unmolested lives, wolves as a species had a right to live in their ancestral lands. Arthur Carhart's letter to Stanley Young put it this way, a year after publishing *Last Stand*: "Isn't it a just consideration that the cats and wolves and coyotes have a damn sight better basic right to live in the hills and have the use of that part of the world as their own than the domestic stock of the stockmen?" (Robinson 2005, 222-223). Richard Nixon's Special Message to Congress presenting the 1972 environmental program alluded to rights of wilderness as a whole: "Wild places and wild things constitute a treasure to be cherished and protected for all time. The pleasure and refreshment which they give man confirm their value to society. More importantly perhaps, the wonder, beauty, and elemental force in which the least of them share suggest a higher right to exist—not granted to them by man and not his to take away" (Nixon 1972). Leo Cottenoir, who killed the last wolf in Wyoming in 1943 under the impression that there were others in the area, said in a 1990's interview: "The wolf is

[7] Boas's book in 1911 explained the labeling of modern human cultures as "noncivilized", "inferior", or in the lower stages of "some uniform evolutionary sequence" as a product of racism rather than observation; differences between modern languages were a result of their environments, not mental and physical differences between groups of humans (Radick 2007, ___after 187).

one of God's creatures and has as much right to be here as any other animal. They are a native animal, native to the country and something that has always been there. Why do stockmen think that livestock has more of a right to be here than the wolves?" (McIntyre 1995, 285). This echoed Henry Shoemaker's older theological motive to protect both the wolf's "inherent right to live" and biodiversity in general: "No person stopped to reason if the wolves had a useful purpose in the world—man deliberately acted as if the Wise Maker had erred in creating such animals. All living things have a *purpose;* it would be a loss to the world if even the common house flies were completely exterminated" (Shoemaker 1914, 9-10).

Respect for wolves' right to exist never fully disappeared from America even when it was swamped by the dominant narrative of manifest destiny and extermination. Manuel Iron Cloud (Oglala Lakota) learned from his grandmother to see wolves as a nation which deserves the same rights as any other. This grandmother lived in the Dakotas at the same time as Ben Corbin (Iron Cloud 1995). While power relations in economic and racial politics drove pro-extermination attitudes to prominence, relationships between humans and wolves in America were never homogeneous.

In a 1992 lecture, Sicangu Lakota historian Joseph Marshall III articulated the parallel story of wolves and Native Americans:

> For centuries, the Wolf and the Native American shared time, space, and life in North America. They also shared the same fate. The European newcomer considered both Wolf and Native American the antithesis to all he stood for, never really bothering to look sincerely beyond the obvious differences. He drove the Wolf and the Native American from ancestral homelands, disrupted their lives, and upset their balance. Life was never the same. By the late nineteenth century, wolves were rare below the 48th parallel. By 1900, the Native American population had dropped from several million to 250,000.
>
> The Wolf and the Native American will never again have access to this entire continent. Our lifestyles are, and will continue to be, restricted. While we once

> roamed free over all of North America, the boundaries of our present and future existence can now be measured in scant miles or in a few hours of travel. With that perspective, Indian reservations and national parks have much in common. (Marshall 1992).

While the American war on wolves has officially ended, many wolves live in exploited populations while dealing with fragmented habitat and the disconnect between their normal ecology and the artificial borders imposed by national parks, wilderness areas, and wildlife refuges. These are obstacles for wolves as well as for researchers attempting to understand them. By the time protections for wolves were enacted and humans developed an interest in them as wildlife themselves (as opposed to 'predators that eat the wildlife'), much of wolf research was forced to rely on observing the animals in a disrupted and ahistorical context.

Early Wolf Research and Ongoing Projects

> *The pursuit of science solely for its own sake, however commendable it may be, is not the spirit that animates our government in its support of scientific research. In its aims and ambitions this is a practical age. Thousands of men are experimenting, inventing, and prying into the secrets of nature for the avowed purpose of utilizing their discoveries for the practical benefit of mankind.*
>
> – Henry H. Henshaw, chief of the US Biological Survey from 1910-1916

From the beginning, American wolf research has been influenced by a utilitarian approach to ecology. Many people read *Thinking Like a Mountain* and want to interpret it as a story about Leopold learning to have respect for wolves for their own sake, but the way Leopold describes it, looking into the dying wolf's eyes did not grant him a sense of respect for the wolf as an individual or the pack as a social group, but only their utility as a keystone predator in the ecosystem. Coleman describes it as taking a position against the Biological Survey's

extermination of "useless" animals in the name of conservation, but also a realization about the "usefulness" of wolves (Coleman 2004, 221).

The survival of questions depends on selection at two levels: one that determines which questions get asked in the first place and another that determines which questions get researched (i.e., which questions get funding). Both levels, especially the latter, tend to favor questions about how things can benefit humans. Henshaw noted this in the early days of the war on wolves, when government research on predators was primarily research on predator extermination and when scientists were not only allowed but encouraged to credulously believe stockmen's claims about wolf depredation. After the humans' goals changed to preservation and conservation, wolf studies began to focus on population health, predator-prey ecology, and how to manage interactions with humans and livestock. Especially in places where wolves were endangered and exploited, there was no time or money to spare on studies of wolves in the wild[8] that weren't primarily about population ecology. This is not to say that basic research for the sake of the wolves themselves didn't exist; but it was (and is) rare to introduce a study with an emphasis on understanding wolves on their own terms.

Even today, studies of wolves in human-dominated locations often focus on management. Research on Yellowstone wolves since their reintroduction has been largely confined to ecological studies of how wolves fit into the food web such as how their reintroduction in 1995

[8] Behavioral research was often confined to studies of captive wolves, but in the absence of normal family dynamics, cooperative hunting, travelling, and interacting with other species, captive wolves were not very informative about social questions.

caused trophic cascades in which riparian ecosystems were able to recover from overbrowsing (despite a unique opportunity for behavioral research in a population that is more accustomed than most to seeing roads and human observers), and many papers on wild animals in general are framed in terms of how their questions and conclusions relate to human evolution. There have always been exceptions to these trends, but ecological concerns surrounding what humans can do to aid wolf recovery and to avoid human-wolf conflicts remain emphasized in the wolf literature over questions about individuals, behavior, and communication.

In 1939, NPS biologist Adolph Murie was assigned to study the relationship between wolves and Dahl sheep at Mt. McKinley (Denali National Park) for part of a series on "Fauna of the National Parks". His 1944 report, *The Wolves of Mount McKinley,* is often cited as the first modern field study of wolves in their evolutionary context. The majority of the book describes predator-prey relations and other aspects of ecology, but the section on wolf behavior contains long-term observations of several packs and descriptions of hunting, social, and communicative behavior. Murie had no previous wolf observations to draw on and wasn't working with a pre-existing ethogram or conventional ways to describe wolf behavior. His descriptions of a pack rallying are fairly objective and exemplary of most of his accounts of behavior: "they all howled and there was considerable barking which resembled the yapping of coyotes", "much tail wagging and milling around" (Murie 1944, 38). He was not unwilling to assume motivations and describe actions and personality attributes using words like "solemn", "dandy", "attentive", "friendliness", "concern and responsibility", "peering searchingly at us", "examining us intently", and "begging quarter"; but while some of these phrases would draw objection today, *The Wolves of Mount McKinley* provided one of the first accounts of wolf behavior and predation

largely free of anthropomorphic biases one way or the other: a book that did its best to describe wolves objectively and on their own terms. It was published in 1944, but largely ignored outside of Alaska at the time (Gipson 1995). Instead, *The Wolves of North America* by Stanley Young and Survey biologist Edward Goldman (published in the same year as Murie's) "passed as the only authoritative general work on wolves in America or Europe until the 1960's" (Lopez 1978, 223). Goldman's part of the book was taxonomy and served as the best source available on wolf taxonomy for several decades, but Young's part on predation and natural history included speculations and erroneous information (Gipson 1995).

Sigurd Olson published a paper on wolf ecology with a focus on predatory relationships in 1938, which is more properly the first serious field study of wild wolves as he was five years ahead of Murie. Olson was an independent researcher working in the Superior National Forest and relying on accumulated hours of observation while following wolves on showshoes. Like Murie, his work was basic ethological research meant to obtain a baseline level of knowledge about how wolves actually function in the wild: a lot of observation of wolves in their evolutionary context and no experiments of studies with manipulations. Olson emphasized the integrity of the "original" or "natural" state of a place or an ecosystem. Studying in the SNF, where wolves remained because previous humans had been uninterested in the land with little agricultural potential, he could observe what he considered real natural conditions that could provide "a true picture of predatory relationships in an undisturbed situation" (Olson 1938).

Describing his observations in *The Wolves of Mount McKinley*, Murie said "it was an inexhaustible thrill to watch the wolves simply because they typify the wilderness so completely" (Murie 1944, 29). But, like wilderness itself, Murie talked about wolves as obsolete

outside of “areas dedicated to preserving samples of primitive America”. In the foreword to *The Wolves of Mount McKinley,* just before quoting Stanley Young, Murie says: “But the wolf is a powerful animal, and a cunning one, and unfortunately has run counter to the economic interests of man in settled regions. The war against the wolf on our western plains, when cattle replaced the buffalo and the wolf became a serious menace to the livestock industry, is an interesting phase of early western history. *It was of course necessary that the wolf should go from those regions* [emphasis added].” He also echoed Young’s opinion that wolves should be kept “in wilderness areas where there will not be interference from economic interests” (Murie 1944, XIII-XIV). Murie and Olson used similar methods and made similar observations, but Murie’s status as a government employee may have affected his final interpretation of the desired relationship between humans and wolves. He introduced one of the first scientific studies of wild wolves by reciting a Survey message that the war on wolves was necessary for the progress of civilization as was the conversion of wilderness into a tamed landscape. Murie’s successor in Denali, Gordon Haber, had more academic freedom as an independent researcher with varying sources of funding; his recommendations were not based on what was convenient for humans and consequently he was considered a constant thorn in the side of Alaska Fish and Game (Haber & Holleman 2013, 12).

Early wolf studies helped to clarify some questions about wolves as predators, but the most important information about how wolves hunt came from the first observations of wolves from the air. The Isle Royale project, started by Durward Allen in 1958 and taken over by Rolf Peterson in the 1970’s, allowed humans to dispel popular myths about wolves as predators. Before planes were available, it was difficult for humans to see wolves make a kill. Wolves are

mainly crepuscular predators (Theuerkauf et al 2003) and were often shrouded from the view of early colonists by trees and hills. The colonists "imagined squadrons of wolves, coordinating their attacks with barks and howls" (Coleman 2004, 75), and rumors about the viciousness of wolf kills proliferated throughout European-American culture from then on. Until the 1950's, it was a common belief that wolves took down their prey by hamstringing them[9] despite the lack of evidence of such injuries on wolf-killed carcasses. Even later, during the government extermination program, wolves stopped returning to their kills in most regions of the U.S. This cultural change among wolves in exploited populations developed because old carcasses were often poisoned or set with traps (as Survey employees tried to poison every carcass they found for several wolf generations), so only new kills were safe to eat. Hunters, ranchers, and federal wolfers seized on this behavior as proof of wastefulness, a moral failing apparently punishable by death (McIntyre 1995, 19-20).

Ecological research on wolves as predators revealed that wolves primarily go after vulnerable individuals and that they often return to feed on old carcasses or scavenge from winter-killed animals[10]; aerial observations also led to the discovery that wolves only kill about

[9] In one outlaw wolf story from Lewistown, MT, it is claimed "none could doubt the maimed and dead cattle left behind, hamstrung, tails bitten off, and often still living though a meal had been taken from a hind quarter" (Wineman 1930); similarly, a story from Roundup, MT says that in the 1800's "the predators would leap on the backs of the cattle or try to ham string them" (*Horizons* 1974).

[10] About 50% of carcasses wolves ate in Denali during Haber's study were kills and the other 50% were scavenged. During severe winters, up to 85% of wolves' diets can be comprised of scavenged winter kills (Haber & Holleman 2013, 143).

10% of the animals they confront[11] and that they spend time testing prey animals before deciding to go for a kill. While they do not use howls or barks to coordinate during a hunt (McIntyre 2016), they will howl before and after hunting to rally or reunite the pack and they may use quiet contact vocalizations to stay together when travelling (Smith 2019).

Independent researcher Gordon Haber, who worked from 1966 until his death in 2009, can be considered a direct descendant of Murie. Murie first introduced Haber to the wolf packs in Denali, and between them the two accumulated over 70 years of continuous observation of a few groups including the Toklat family, which was one of the oldest known nonhuman social groups in the world until it split due to human exploitation in 2010. Because interior Alaska escaped the Pleistocene glaciations, the wolf population in the area already had a longer continuous history than other populations in the world, and remained relatively stable with non-migratory prey[12] even with some human exploitation, so it was an ideal population for studying the cultural characteristics of long-lived groups (Haber & Holleman 2013, 25-27; 238). Haber spent as much time as possible observing from the ground and later from planes and with the

[11] In *The Wolves of Isle Royale* (1966), Dave Mech found that wolves killed 7.8% of the moose they tested. Other estimates of winter hunting success range from 1-56%, depending on the location and prey species. In Denali, 5-9% of encounters with moose resulted in a kill, depending on snow depth (Haber & Holleman 2013, 136). Winter success rates are expected to be maximal, as herbivores are both weaker from lack of food and more vulnerable due to the difficulty of running in snow, which wolves can often run on top of using the wide surface area of their feet (Mech & Peterson 2003).

[12] Modern wolves have been relatively unchanged for 1 million years, while moose have only been a prey source for 100,000 years; wolves had longer histories with other prey species including wapiti (North American elk), bison, caribou, deer, and several Eurasian elk species (Theberge & Theberge 1998).

ability to track wolves with NPS collars. Planes and radiocollars[13] allowed Haber to observe more family groups, social relationships, and culturally transmitted behaviors in what was for a time one of the few relatively non-exploited and continuous wolf groups. He found that the main functional unit of wolves is not the individual but the pack or family and confirmed the importance of intact groups with experienced individuals for cultural transmission, learning, social cohesion, and ecological function.

In the 1950's, Isle Royale became available as an accessible and contained wolf population. Canadian wolves crossed the Lake Superior ice to hunt moose on the island in the late 1940's. Durward Allen began the ongoing ecological study of Isle Royale in 1958; at that time wolf predation on moose was mostly compensatory, but in later decades populations fluctuated and wolves became an important check on the moose population and management of vegetation. This study has since provided important information on predator-prey dynamics and interactions among trophic levels in a contained island with minimal variables. (Steinhart 1995, 61-66; NPS 2018). Questions on Isle Royale have always been focused on the ecology of moose predation (and more recently on population genetics); while long-term observers accumulate knowledge about wolf behavior, it is not a focus for funding on Isle Royale[14].

[13] Haber had doubts about collars after the NPS killed 3 wolves in collaring accidents, possibly by accidentally loading the wrong tranquilizer into the dart (they carried doses for moose in similar cartridges); the collaring deaths of key individuals caused packs to splinter, leading to the deaths of other members (Haber & Holleman 2013, 186).
[14] By the winter of 2017-2018, the population of wolves on Isle Royale fell to 2 and increasing unpredictability of the Lake Superior ice meant that recolonization from the mainland was unlikely, so the NPS reintroduced wolves who have now formed groups, and it is likely that pups were born on the island in 2019 or 2020 (NPS 2018, 2020).

Dave Mech was a student of Allen in the late 50's and early 60's when he took over the Isle Royale study; his doctoral thesis was published as *The Wolves of Isle Royale* by the Department of the Interior within the same "Fauna of the National Parks" series as *The Wolves of Mount McKinley*. He then went to the SNF and studied predatory relationships of wolves and deer as well as the effects of ecological conditions like snow depth on vulnerability (Steinhart 1995, 70-71). Mech is now one of the world's top wolf researchers, and continues to run the long-term study in the SNF. When he published *The Wolf* in 1981, it replaced Young and Goldman as the standard reference on the species (Steinhart 1995, 67). In 1985, Mech founded the International Wolf Center, a research and education organization centered in Ely, MN. Mech has studied other wolf populations including Yellowstone, Denali, Ellesmere Island, and Nunavut; he mainly studies predator-prey interactions but has also studied social ecology and interactions within packs (Breining 2004).

Another population that escaped the war on wolves is Algonquin Provincial Park in Ontario, the subject of a discontinuous but long-term study which John and Mary Theberge took over from Doug Pimlott in 1987. John Theberge's 1966 thesis was on communication by howling in Algonquin Park, and he continues to research howls and vocal communication along with ecology, predation, and wolf-human relations.

Doug Smith studied under Rolf Peterson on Isle Royale, worked on wolf research in the Isle Royale and Minnesota populations from the late 70's to the 90's, and led the Wolf Restoration Project in Yellowstone. Smith is now the senior wildlife biologist in YNP and leads the Yellowstone Wolf Project. The YWP was launched with the 1995-1997 reintroduction and stands as a long-running project with 25 years of continuous data on wolf ecology including

movements, territories, predation, reproduction, disease, pack structure, and trophic cascades. The project uses GPS collars, tracking collars, ground observations, and planes. Yellowstone wolves are a uniquely accessible and visible population, especially the packs living in and around the Lamar Valley, and this attracts amateur wolf watchers as well as researchers from other projects and short-term studies. 145 research permits were issued in 2019, of which 46% were for biology and ecology. All these long-term projects are essential for ecological study. "When you're looking at population changes in a long-lived species that are elusive to begin with, it takes a long-lived study to get results," Mech said about wolves and deer in Minnesota, "but budgeting is done on an annual basis in the government" (Steinhart 1995, 119).

Yellowstone Wolves

When Yellowstone was designated the first national park in the world in 1872, it was preserved because of the tourist attractions formed by the unique geology (the "natural curiosities" such as geysers and hot springs). Park designation did not spare Yellowstone from the wolf war; the last wolf in the park was killed in 1926, and it remained without this keystone predator until three groups were reintroduced in 1995 (Smith & Ferguson 2012). The idea that national parks should be places to preserve wilderness surfaced in the late 19th century, leading to the formation of more parks through the 1890's and changes in the management of existing parks (Robinson 2005, 52). Even when parks were meant to be sanctuaries for wildlife, wolves were still excluded from the category of "wildlife" and even killed in the name of wildlife preservation. Durward Allen explained this phenomenon in 1954: "to them a carnivorous animal is not wildlife; he is the enemy of all honest wildlife. The wolf doesn't live in the forest; he infests it. You don't just kill a predator; you execute him. You don't hunt him for sport; you

track him down in a crusade for moral reform" (Nelson et al 2010). Parks and game refuges were "administered as herbivore sanctuaries" (Olson 1938) until more humans began to show a desire for primitive or pristine landscapes.

> With the fast-growing appreciation of the true meaning of wilderness, we are beginning to question the idea of the total elimination of predators, realizing that, after all, lions, wolves and coyotes may be an exceedingly vital part of a primitive community, a part which once removed would disturb the delicate ecological adjustment of dependent types and take from a country a charm and uniqueness which is irreplaceable. To go into a region where the large carnivores are gone, to see hoofed game with its natural alertness lacking, to know above all that the primitive population has been tampered with, is like traveling through a cultivated estate. Wilderness in all its forms is what the true observer wants to see and with this realization dawns a new appreciation of carnivores and the role they play (Olson 1938).

The superintendent of Yellowstone stated this position clearly at a conference in 1932: "we have always assumed, whether rightly or wrongly, that the elk and the deer and the antelope were the type of animal the park was for. We have had the support of the game associations only on the basis that the parks would act as reservoirs for the game and the increase would overflow and form legitimate hunting." When national parks were a new concept, their continued existence required on political support from influential groups, including sportsmen's associations representing humans who desired to replace at least some of the native predators (McIntyre 1995, 214-215). The idea of administrating parks as game refuges was not a reflection of an existing public opinion on what parks should be for, but a political move meant to ally a new institution with powerful groups.

The gray wolf, extirpated from the lower 48 except for some parts of Minnesota, was first listed as endangered under the Endangered Species Preservation act in 1967. The ESA passed in 1973 and multiple gray wolf subspecies were listed as endangered in parts of their range; they were lumped into one listing in 1978. In the same year, the first study examining a possible

reintroduction was submitted to the Department of the Interior. The Northern Rocky Mountain Wolf Recovery Plan from the FWS was approved in 1980 and revised in 1987 to propose an introduction of experimental-nonessential populations[15] in Glacier/Bob Marshall Wilderness, YNP, and central Idaho. The record of decision was signed in 1994 after the completion of the EIS. Wolves were captured from areas of Alberta and British Columbia with similar terrain and prey to Yellowstone and kept in acclimation pens in the park for 10 weeks (Phillips & Smith 1997). The reintroduction to Yellowstone in 1995-96 marked the beginning of the Yellowstone Wolf Project and began a new surge of wolf research in a uniquely accessible area where wild wolves are often visible from roads and trails.

In 1959, Frank and John Craighead began a 12-year study of Yellowstone's grizzly bears using radiocollars to track their movements and map their ranges. Their team developed the first radiocollars that were able to track large mammals. This began the discovery of the Greater Yellowstone Ecosystem and forced humans to realize that their invented park boundaries had no natural justification. Animals protected within the park regularly utilize resources outside its boundaries and rely on them for their survival. It should be no surprise that the boundaries of a park originally formed to attract sightseers to its geothermal features have little to do with the ecological realities of the species within it. Even after the park's main purpose became oriented

[15] The experimental-nonessential designation meant that wolves from these groups who left the park and preyed on livestock could be killed or relocated. Some humans pushed for the reintroduction of experimental populations for this reason, even though there had been several sightings in the decades since extirpation implying that wolves might have soon been recolonizing the park naturally (Steinhart 1995, 243-246)—a naturally recolonizing population would be fully protected by the ESA, while an experimental population is more 'controllable'.

toward the preservation of animals and ecosystems as well as recreation and tourism, changing the park borders to suit the actual ecological needs of its intended beneficiaries was a political impossibility. The conflict between patterns of land use by animal populations and political boundaries which dictate human activity affects wolves throughout the country. Wolves can disperse long distances and regularly travel routes within their territories, patrol borders, and make excursions outside.

In Yellowstone, the biological irrelevance of the park borders is apparent in disruptions of packs caused by the shooting of wolves in areas adjacent to the boundaries. A solution to this problem is to create a buffer zone to protect wolves around the park, but the establishment of a permanent buffer zone was outlawed in 2013 by the Montana State Legislature ("In an area immediately adjacent to a national park, the commission may not prohibit the hunting or trapping of wolves or close the area to wolf hunting or trapping unless a wolf harvest quota established by the commission for that area has been met"; MT HB 73, 2013). Instead, the Fish & Wildlife Commission must consistently vote on harvest quota of zero every year in hunting zones adjacent to the park in order to create an effective buffer. In February 2020, the Montana Fish & Wildlife Commission voted to reduce the quotas from two to one in each of the districts bordering YNP (Reilly 2020). Quotas of zero are difficult to achieve because of pressure from hunting groups claiming that wolf hunts preserve deer and elk populations.

Management of wolves and humans around Yellowstone faces the same barriers as management in Denali. Gordon Haber observed in 1991 that "most biologists still take a superficial, numbers-based view of what constitutes a healthy wolf population … The problem is that wolves have complex societies. It takes a long time, at least several generations, for a family

group to reach its societal cruising speed" (Steiner 2012). Using this numbers approach, the Alaska Board of Game concluded that the wolf population would still be sustainable if they refused to extend a buffer around a region of land jutting into the park[16]; they even got rid of a partial buffer that was established in 2000 and put a moratorium on buffer proposals after the NPS proposed an expansion in 2010 (Haber & Holleman 2013, 191-192). With the elimination of the partial buffer, humans set traplines as close to the border as they could, and long-lived family groups fragmented and disappeared. The Game Board insisted that there were enough wolves to repopulate the area—ignoring the social disasters that resulted from trapping and the impossibility of maintaining a long-lived pack with cultural stability in a heavily exploited area.

Alaska was plagued by arbitrary units and delineations. They counted wolves in Denali park, which is not an isolated gene pool and therefore not a population. But because the number of wolves in the genetic population had nothing to do with management in Denali, and because managers were unwilling to keep track of the social and ecological units (packs), they based their decisions on a number that is meaningless in the real world. The same was true for prey animals. Managers map out arbitrary management units unrelated to prey distributions and determine whether to shoot wolves or allow more hunting of ungulates based on whether the animals

[16] This region, the Wolf Townships, was "an essential and regular part of the wolves' natural ecosystem territory" (Haber & Holleman 2013, 192). It looks like a rectangular peninsula protruding into the park. Alaska and the NPS protect Denali caribou on state and private land outside the park, but the Game Board was unwilling to extend the same protections to wolves within their own territories. Aside from political tangles that make otherwise straightforward management situations complicated, this also demonstrates how dependent wildlife populations are on human-drawn borders that have nothing to do with the ecological reality of the place and its inhabitants.

censused in the units fall above or below an arbitrary number (Haber & Holleman 2013, 216-218), despite knowing that populations are supposed to fluctuate thanks to a multitude of studies on predator-prey dynamics. Yellowstone has the same problem: Fish & Wildlife managers have repeatedly expressed the desire to manage wolves "like any other animal", only wanting to look at population numbers despite the social nature of the species (Ilona Popper, personal communication). Most packs range outside of park boundaries and are susceptible to poaching and legal hunting near the borders. The death of one experienced or charismatic member of a pack can result in loss of important knowledge about how to survive in their territory, breakup of the pack, and deaths of other members deprived of support in hunting, defense, and pup care.

While research uncovers ecological and social realities about wolves with clear implications for how they ought to be managed, political artifacts such as borders and legislations hinder their application. Changes in human activity do not emerge from a linear process starting with research which produces facts which produce decisions which produce actions. They are governed by a constant exchange of influences between science, culture, and politics as well as the institutional dynamics that affect all three. Institutional, political, and cultural factors determine what kinds of scientific paradigms become normal, what questions can be asked, and what kind of evidence is admissible. Political tradeoffs, institutional structures, and cultural biases determine when, where, and what can be done with scientific results/conclusions. Well-publicized research increases knowledge within the public and affects cultural perceptions of wolves, making people less fearful and allowing the public to compare management recommendations from scientists with what politicians and managers actually do. Stephen R. Kellert identified access to science education as a key factor that decreases utilitarian,

dominionistic, and negativistic valuations of nature (Bekoff 2002, 44). Reactions from the public can affect what is possible politically.

One question that has not received much attention in Yellowstone is that of cultural changes in the 25-year-old population. Historians like Jon Coleman and Brett Walker apply biology to history, but in the case of studying cultural evolution in wolves, history should be applied to biology. Wolves with similar genetics inhabit a wide variety of habitats worldwide. Culture is quicker to adjust to changing environments than genetics and allows the behavior of social groups to adapt faster than it could via natural selection alone. Studies like Haber's that monitor behavior over generations in multiple populations would provide insight into how learned behaviors develop, how much is due to biological vs. cultural evolution, and the influences of environmental factors on both kinds of change. Yellowstone is a unique environment with the potential to foster new cultural phenomena, yet it remains difficult to get attention on cultural or behavioral questions. Steinhart quoted a researcher on why behavioral studies aren't usually funded: "the question of raised-leg urination might be interesting, but no game agency is going to fund it. They want to know what the effects of predation are on an ungulate population" (Steinhart 1995, 119). There has been some shifting since the 90's as the burning management questions were answered and wolf populations stabilized, but Doug Smith confirms that despite the accessibility and popularity of the Yellowstone wolf packs, there has been "very little work on behavior" in Yellowstone wolves over the last 25 years and the amount of behavioral research has always been low compared to that on ecology (Smith 2019).

Reintroduction and the aftermath of the wolf war created an environment in Yellowstone that shapes the wolf research that takes place in the park. Studies of population ecology are prioritized in the YWP's long-term study over behavior and communication. Parks like Denali and Algonquin, where wolves were never extirpated and reintroduction was never necessary, have fostered more delving into behavioral questions. As early as the 1960's, Theberge was able to devote time to questions about communication and howling in Algonquin; and Haber recorded behavioral and cultural patterns during his long-term study of wolves in Denali.

The meaning of Yellowstone's wolves to humans is situated in a matrix of ideas and historical background on wilderness preservation, the value of species, the nature of ecological networks, and the politics of predation and agriculture. The research topics granted the most time and resources in the park reflect what people believe to be most important about Yellowstone wolves. Humans look to Yellowstone wolves to discover the ecological impacts of reintroducing predators to an unbalanced system, to monitor the movements of individuals and packs on a territorial landscape, and to watch changes in pack composition and how it affects hunting and defense. While the park contains packs with known histories and genealogies which have been monitored by radiocollars and under observation since the reintroduction, questions about communication and cultural change in behavior patterns after several generations of living on the Yellowstone landscape are rare. To humans—at least to the ones capable of funding wolf research—the significance of Yellowstone wolves is that they are primarily subjects of an ecological story of extirpation, reintroduction, recovery, and controversy.

CHAPTER TWO

HUMANS STUDYING COMMUNICATION

Contemporary studies of wolf howls exist amid a background of paradigm shifts which have determined which questions are askable and which disciplines questions fall into at different times. The first section of this chapter will show how ethology shifted away from puzzle-box comparative psychology and emphasized observation and explanation of behaviors in evolutionary context. The second section will provide an overview of topics and foci in animal communication research in order to provide a context for asking semantic questions about wolf howling and explain the sources of methods and technology that have been recruited for answering wolf howl questions. The third section will discuss the ongoing debate about the definition and uniqueness of language, the efficacy of the language debate, and why it exists in the background of every communication study and especially those concerned with semanticity.

Context in Ethology

Ethology has been the discipline in biology most interested in the study of animal communication in an evolutionary sense. The word "ethology" was applied by Isidore Geoffroy-Saint-Hilaire in 1859 to "the study of animals as living beings in their natural environments" (Smith 1977, 3) or "the characters of animals in their natural habitats". Isidore Geoffroy-Saint-Hilaire was the son of Étienne Geoffroy-Saint-Hilaire, who had unsuccessfully argued against Georges Cuvier's laboratory-based methods and for the naturalistic study of animals in 1830 (Jaynes 1969). While the Geoffroy-Saint-Hilaires wanted to study the nature or character (ethos)

of animals from a naturalistic perspective, their evolutionary paradigm was based on a uniform plan of composition throughout species (Jaynes 1969) rather than natural selection, so the contemporary meaning of ethology in a Darwinian framework — the study of behavior in its evolutionary context, with the purpose of discovering how and why behaviors are adaptive in their environments — was not fully developed. Ethology would discuss behaviors as characters that could be used for taxonomy just like morphological characters and considered part of a species' adaptive arsenal.

Naturalistic observation went out of fashion for a time when most behavior study returned to laboratories following Cuvier's experimental comparative-psychology-based approach (Smith 1977, 3). Nineteenth-century biology focused on comparative anatomy in an effort to make itself as technical (and funding-worthy) as physics (Jaynes 1969). Increasing technicality is often a sign of controversy within a field (Latour 1987), but in this case it was a result of competition between subjects in an atmosphere that revered controlled experimental methods with complex quantitative results. Early ethology emerged from this environment and included a lot of work on instinctive behaviors and how they were triggered in and out of evolutionary context. By the 1970's, ethology had moved away from focusing on instinct, motivation, and releasers and toward more broad questions, many spawned by Tinbergen's four aims (Burghardt 2013). Niko Tinbergen, Konrad Lorenz, and Karl von Frisch won a Nobel prize in 1973 for their behavioral research on ethology and social behavior.

North American ethology in its present form materialized in the 1940's after World War II, but was not clearly defined in its inception. In the 1930's and 40's, animal cognition and behavior were covered under zoology, physiology, and psychology, but psychologists were

studying things like learning in animals only because they were interested in harnessing knowledge to apply to humans. Ethologists asked how behaviors, both learned and instinctive, functioned for animals. Niko Tinbergen opened his 1963 paper "On aims and methods of ethology" with what he called the easiest definition of ethology, "the type of behavior study which was given a strong impetus, and was made "respectable", by Konrad Lorenz". Lorenz in turn once defined ethology as "the branch of research started by Oskar Heinroth". Tinbergen listed several scattered definitions he'd heard for the "science in its infancy", including "the study of releasers" and "the science of innate behavior", and assessed the state of ethology as "very far from being a unified science" before putting forth his own definition.

Tinbergen posited four aims for ethology: three that Julian Huxley, evolutionary biologist and grandson of "Darwin's bulldog" T. H. Huxley, had called the major aims of biology (causation, adaptiveness of 'survival value', and evolution) and a fourth which Tinbergen added to the list (ontogeny). These continue to characterize descriptions of ethology and research programs through the present. His goal was to synthesize ethology as the biological study of behavior (applying "biological thinking" to behavior as opposed to purely psychological behaviorism); the study of behavior with respect to evolution. Lorenz was crucial because he "made us look at behaviour through the eyes of biologists" (Tinbergen 1963). While behaviorists were looking for "the prehuman in the animals" (Tinbergen quoted in Radick 2007), ethologists were studying animals for their own sake and only later identifying the animal in the humans.

Tinbergen characterized early ethologists by their "wish to return to an inductive start", to go back to the basics of observation and description and to the general question of "why do these animals behave as they do?". They were naturalists familiar with a variety of behaviors not

mentioned or studied by behaviorists, reacting to a trend in psychology of skipping the descriptive phase, focusing on "a few phenomena observed in a handful of species which were kept in impoverished environments", and attempting to formulate and test general theories based on this wobbly foundation. They were also reacting against a trend in biology that focused on the structure of organs at the expense of function. From Tinbergen in the 60's to Marc Hauser in the 90's and E. O. Wilson to this day, ethologists have emphasized the descriptive, natural-history phase of research and discouraged abandoning observation during the analysis phase. This pushes back against a trend that was popular even within ethology in the late 1950's in which collecting observations was not considered part of the science (Tinbergen 1963). Observation, natural history, and basic descriptions are what allow the formulation of hypotheses and experiments that make sense. Time spent observing behavior in the wild has the potential to reveal that one's experimental or analytical paradigm rests on false assumptions and prevent researchers from wasting time on bad assumptions about evolutionary history or lab phenomena that are irrelevant to the wild. A lot of research focuses on adaptiveness, and basic observation of wild animals is necessary to see how behaviors function in context.

According to historian Gregory Radick, early ethologists like Lorenz, Tinbergen, W.H. Thorpe, and Peter Marler "defined their science *against* comparative psychology, or, more precisely, against a caricature of that science" (Radick 2007, 9). By the time ethologists were defining their field, comparative psychologists had narrowed theirs into a restrictive paradigm based on the study of associative learning by a few domesticated species in artificial laboratory environments. The dominant paradigm in comparative psychology was based on Edward Thorndike's puzzle-box experiments; a large percentage of comparative psychology papers were

on maze-learning and conditioning in white rats, with results presented as graphical learning curves and interpreted according to Morgan's canon (Radick 2007, Burghardt 2013).

Lorenz remarked in 1950 that the name of the Journal of Comparative Psychology was ironic given that it had never actually published a comparative paper (Burghardt 2013), but even in the 40's, comparative psychologists were in dialogue with ethology and beginning to re-evaluate how their work related to evolution. By 1970, some synthesis between ethology and comparative psychology emerged. Ethologists were asking some questions with experimental answers and comparative psychologists did more systematic field studies and documenting of behavior in the wild. An interest in primates developed in the 1970's and continued into the 2010's. Around the same time, there was a move away from behavioral homologies and phylogenetic origins and toward questions about how behavior is adaptive within recent ecology (social ethology, socioecology, behavioral ecology, and sociobiology). While the field is now more focused on evolution, adaptation, and things like cognition and communication, there is no doubt that the Thorndikian caricature was representative of the dominant paradigm throughout American psychology during the first half of the 20th century.

More recently, ethologists have become interested in the kind of psychological questions that can't be answered in a behaviorist mode. In 1997, Gordon Burghardt proposed adding a fifth aim for ethology to Tinbergen's four: private experience. This is the question which behaviorists attempted to eliminate due to the perceived impossibility of knowing anything about another organism's subjective experience, but opening it back up and reintroducing it into the space of possible questions allows us to ask about things important to the understanding of communication. Aspects of private experience include the qualia of mental representations,

intended and perceived meanings as opposed to functional reference, and the general nature of the intentions behind communication behavior. In some papers, these things are mentioned but left alone as the methods do not allow the authors to come to any conclusions about them. In others they are not mentioned at all, but their absence is conspicuous. While these objects are far more opaque than functional reference and structural description, it is important to keep them in mind when developing research questions and methods that may be able to probe the subjective experience and intentions behind behavior and communication (Burghardt 1997).

This difficult question can be interpreted as a return to the 1978 foundations of cognitive ethology when Donald Griffin, inspired by Thomas Nagel's 1974 paper "What Is It Like to Be a Bat?"[17], published *The Question of Animal Awareness*. In a 1999 symposium on animal consciousness at the Annual Meeting of the Society for Integrative and Comparative Biology, Griffin warned against "paralytic perfectionism". In an effort to be sufficiently rigorous to keep up with sciences like physics and chemistry in the public image, biologists and psychologists have sometimes built up standards of proof that close off entire fields of study. This was the reason for the rise of behaviorism: because subjective psychological processes are difficult to study and can never be observed directly, they were banned from consideration. In other

[17] Nagel discussed how if an organism has conscious mental states, there is something that it is like to be that organism, but extrapolating from one's own experience fails to capture the subjective experiences as they happen in the other organism's mind; he ends on the idea that approaching the subjective-objective problem from the objective side may allow a closer understanding of mental phenomena that approaches the ability to describe a subjective event to an organism incapable of experiencing it, such as explaining what it is like to be a bat to a human who cannot fly or use echolocation, or explaining what it is like for a to see colors to a blind human (Nagel 1974).

sciences, Griffin points out, progress is made when people focus their study on the more difficult questions; we will never be able to directly experience another organism's consciousness, but we cannot gain any understanding of the topic if we allow that inevitable imperfection to stop us from asking the questions in the first place. Progress in neuropsychology, physiology of learning, and communication research has allowed greater access to questions of consciousness in humans and nonhumans alike and should continue to do so if these research questions remain askable (Griffin 2000).

The difficulty or impossibility of knowing what another's private experience is like is not the only barrier to its study. Private experience also triggers a reaction of reluctance stemming from humans' desire for uniqueness. Humans often want to believe that they are the 'most' or 'only' of something—the most intelligence, the richest inner lives, the only introspection, or the only language. Fear of shattering the illusion of uniqueness leads humans to avoid some kinds of animal research, but by studying traits in their evolutionary contexts we can discover why we are the way we are, how and why species with similar environments share some traits but not others, and what connects us to our past and to other species in the present. Keeping private experience in mind even if it is impossible to describe may lead to the discovery that being in good company is more comfortable than standing alone on a pedestal.

The first serious wolf studies around the 1940's occurred when ethology was just starting to become an important discipline in North America, and a few accessible populations have made it possible to observe the same groups of wolves in long-term studies and discover interesting behaviors, ecological relationships, and the transmission of cultural knowledge.

Wolves do not yield much relevant information if studied as isolated individuals in captivity; the functional unit of wolves is the pack and their behavior is based on relationships with pack members, other packs, prey, and geography. The "character" or "ethos" of wolves only exists in a socioecological context. A full understanding of wolves requires ethological study incorporating ecological, evolutionary, social, and cognitive approaches.

Communication Research

An overview of the history of animal communication research will show where wolf howl studies are situated in the current environment. Animal research throughout its history has emphasized different aspects of behavioral evolution. Group-based, individual-based, and gene-based models have all been favored at different times; leading to interest in questions of cooperation, individual competition, competition between genes, and kin selection. Technological developments and the recruitment of technologies for communication research also affect standard methods and askable questions, especially in the realm of vocal communication. There are also trends in focal species and clades. Some questions in communication are weighted heavily toward primates because of an interest in human evolution, others are well-studied in birds because of their easy-to-analyze song structures but newer and more explorative in other animal groups. Particular study species can also influence how researchers interpret their observations and how their results are presented to different audiences, including which species are used for studies about semanticity and cognition.

The ethological approach to communication follows Darwin's *The Expression of the Emotions in Man and Animals* (1872) in which the study of expressions is treated as a branch of natural history viewing expressive displays as traits that can be viewed in an evolutionary

context like any other phenotypic characters. In the 1940's and 50's, during the rise of ethology proper, communication was viewed through a paradigm focused on group selection and ignoring individual competition. A new paradigm in the 1960's turned attention to individual selection and investigated the individual fitness benefits of apparently altruistic communicative actions such as alarm calls, which warn others of a predator but risk drawing the predator's attention to the caller. The 60's and 70's also saw the rise of gene-centered thinking (Hauser 1996, 20-24). Richard Dawkins published *The Selfish Gene* in 1976, reframing natural selection as acting on the gene level. Selection was increasingly viewed through the lens of evolutionary game theory and kin selection (and eventually group selection, in cases where the fate of an individual and their genes depends on the fate of a social group containing non-kin members). Where 40's-50's ethologists focused on communication that evolved to benefit both signaler and receiver, 60's-70's researchers began to think about the effects of cheating or defecting. It would be beneficial for signalers to manipulate receivers such that the signaler gained all the fitness benefit from the interaction, but receivers would evolve to be more incredulous and signalers would evolve to be more convincing, leading to an evolutionary arms race between signalers and receivers. In the 80's, interest in cooperative and competitive interactions balanced out with a recognition that one kind of situation selects for honesty and the other results in an arms race (Hauser 1996, 28-30).

Communication itself has been defined in various ways since the 1970's depending on the writer's study species and specific interests (Hauser 1996, 7). All communication consists of a signaler sending a signal through an environment directed at a receiver who detects the signal and responds to it. It is generally agreed that communication is behavior that has evolved to share information—more specifically, to change the likelihood of another organism selecting

some action from their range of possible actions (a signal is selected for if it causes the receiver to select a response that increases the signaler's fitness). In humans, who can report receiving a signal and its message, researchers are interested in the receiver's interpretation of the signal. In other species an observer only knows that the signal was received if the receiver does something obvious in response rather than just remembering the information for future reference.

Early work on communication and signals was largely behavioristic in that it focused on the signal's presence or absence in relation to stimulus-response mechanisms. These questions usually begin with asking when an animal makes a certain call or display in the wild before moving on to captive studies. With the ability to manipulate specific parts of the signaling environment in the laboratory, people asked about the necessary stimuli to elicit the signal and which specific aspects of the stimuli are sufficient to release the behavior. Treating the environment as containing releasers for signaling behavior led this branch of research to focus on instinctive displays; questions about voluntarily controlled communication emerged later.

Some signals are purely mechanical: the signal contains a stimulus that forces a certain response in the receiver due to the signal's structure and the receiver's physiology, but the receiver is not aware of the content of the signal and does not consciously choose a response. These signals contain information in that they resolve uncertainty in a receiver's subsequent actions, but they do not have any semantic content. Research on these signals focuses on their function as releasers for instinctive receiver behaviors. Lorenz and Tinbergen studied some instinctive responses that have evolved with specific sensory releasers rather than real situations in context, explaining why some responses that appear logical under normal circumstances can

be triggered by unrealistic, supernormal stimuli. Lorenz and Tinbergen found that brooding gulls will react more strongly to unrealistically large model eggs than to realistic model eggs, and herring gull hatchlings react more strongly to a stick with multiple red spots than to a model of an adult's beak, which should have one red spot. In a more variable environment these gulls may have evolved to look for their parents' beaks to get food, but as it is their actual releaser is nothing more than 'thin vertical object + red spot' (Gould & Gould 1994, 27-28). Other signals function by causing the receiver to make a behavioral selection. They transmit information in the form of 'knowledge' such that the receiver is aware of what the signal refers to. A signal of this kind may induce a mental representation of its referent in the mind of the receiver, allowing the receiver to decide how to respond.

These types of signals can be surprisingly difficult to tell apart, and they likely grade into each other depending on the species and type of vocalization. Releasers work when stimuli are highly predictable. In a less predictable environment, it is more adaptive to spend time and energy to comprehend more of the situation and make a more conscious decision, but the amount of choice depends on the demands of the species' physical and social environment. In this context, communication questions diverge between cognitive questions and more behavioristic and evolutionary approaches.

The behaviorist tendency is to only ask about what one can directly observe; the cognitive angle asks more difficult questions but ones that are important for attempting to understand how communication works on a subjective level. Although cognitive questions are harder to answer, researchers do have access to clues in experimental settings and in the wild given enough observation of a multitude of scenarios. Unreliable alarm callers can be ignored,

showing that at least in some species alarm call response is consciously chosen. Calls that occur in less intense situations than alarm calls may be even more useful. For instance, if we observe the food calls of rhesus macaques in only 'normal' scenarios, we might think it possible that the structure of the call simply summons the other group members using an involuntary physiological response with no semantic content or receiver choice. However, upon discovering a group member who has discovered food and not made food-calls, others may attack the food hoarder (Hauser & Marler 1993). This means they know that the food call indicates food, and that if someone found food but failed to make a food call, they must have been concealing the food from everyone else. This behavior, which appears to be an indignant response to cheating, would not exist if the food call was an instinctive summons or if it was not associated with a mental representation of food.

Much recent study of animal communication systems involves describing them in terms of "design features", adaptations, and the relationships between signal structures and functions. Communication work in the 19th and first half of the 20th century was mainly descriptive; later there was a shift towards correlational studies addressing questions about function and the message or content of signals, focusing on attributes of the signaler. A lot of psychological work was done on birdsong with questions about learning: how much of singing is genetic vs. learned in different species, when can learning occur, does learning require feedback or conspecific examples, what happens with experimental manipulations like deafness or only being exposed to other species, etc. (Hauser 1996). The sociobiological turn in the 1970's led most behavioral ecologists to focus on adaptiveness and function, or the ultimate causes of behavior. In the mid-

1990's, communication studies began a return to Tinbergen's four aims and reintegrated questions of mechanisms, ontogeny, and phylogeny (Hauser 1996, 2).

Communication exists in many sensory modalities, but auditory communication is one of the easiest for humans to observe and study. Humans tend to be particularly interested in auditory and specifically vocal communication because their own language is based on vocalizations, although they are also interested in conspicuous visual displays. Some communication research happens outside the human spectrum with auditory signals (ultrasonic bats and infrasonic whales), visual signals (ultraviolet breeding plumage), olfactory signals (especially in insects but also important in most mammals—most of which humans can't smell and can only analyze chemically), and some signals that lie outside of human perception entirely, such as electric fields (Gould & Gould 1994, 20); but most communication research over time has been weighted in favor of things humans can detect, and when it comes to semantic questions, the focus has largely been on vocalizations. Audio recordings and spectrograms are easy to make and analyze, and vocalizations can be "faked" much more easily than some other forms of communication for playback purposes. Auditory communication is a topic for animal behavior and bioacoustics. Not all bioacoustics work on animal vocalizations is about how they function as communication, as studies can use vocalizations to get information about ecology, population dynamics, etc. Wolf howls have been used for these purposes as well as for communication research, and more recently for specific questions about meaning. Communicative and non-communicative studies of vocalizations overlap in methodology and technology including spectrographic analysis and playback studies.

One of the first steps in studying vocalizations or any other signals within a current ethological paradigm is describing their structure, which has been done with wolf vocalizations in increasingly technical ways. Pure description can sometimes be done in captivity (and many short-range vocalizations are exceedingly difficult to hear in the wild), but not all vocalizations can be observed in artificial contexts. The next step is usually to determine the signal's function by observing the behavior of the receiver and figure out how it is adaptive to the sender. This can be done in captivity for some kinds of signals in some species, but usually requires a normal context. For auditory communication, playback studies are the predominant method of assessing what kinds of responses are caused by the auditory signal alone.

The history of playback studies demonstrates how certain questions and methods can fall between the cracks in the space between disciplines. The first playback studies were attempted on primates in captivity and in the wild by Richard Garner in the 1890's, who used one of Thomas Edison's early phonographs; but the method did not fit into any of the biological, psychological, anthropological, or linguistic paradigms dominant at the time. Anthropologists took phonographs into the field throughout the 1890's-1920's, and animal playbacks were a technical possibility, but they failed to catch on outside of bird research until the 1980's when Peter Marler, Dorothy Cheney, and Robert Seyfarth used them to study the functions and messages of primate calls in the wild. The method was reinvented in an ethological framework that hadn't existed in 1890. The playback method was then quickly blackboxed and absorbed into the broader communication paradigm, and it is now found in studies investigating signal responses both in the wild and in captivity.

Another crucial part of the current animal communication paradigm is the spectrograph, a technology that was taken up by bioacoustics after its military development. Work on sound spectrographs, now a requirement for description of any vocalization, was beginning in North America in 1941 for military use in submarine detection. In 1945, spectrographs went public for peacetime uses and were immediately picked up by bird researchers. A Bell radio engineer who headed the military spectrograph project predicted its "opportunity for extensive study" in bioacoustics in 1947: "possibly a study of these [complex animal sounds] could contribute a new chapter to the story of evolution" (Ralph K. Potter quoted in Radick 2007).

Types of vocalizations that are easy to access and describe can lead to taxonomic biases. A lot of research on vocalizations, both in the present and earlier in communication research, centered on birdsong. A song is a vocalization made of fixed, repeating patterns (Payne & McVay 1971). Birds use these displays to attract mates, challenge competitors, and advertise territorial occupation. Songs consist of repeating phrases made of discrete units (often easy for the naked human ear to distinguish in the case of birds, and always distinct on a spectrogram). Birdsong is readily displayed in captivity and its structure is easy to describe. To this day, many papers about mammal vocalizations lead with descriptions of how the same kind of study has already been done in at least one bird species.

Peter Marler, who was instrumental in pioneering semantic studies of mammalian alarm calls, did his first animal communication work was on chaffinch vocalizations in 1948. He described call variation and geographical distribution of song types in terms of trills and phrases (types of discrete units and repeated combinations of units), natural selection (overlapping call

notes are selected against in species with overlapping ranges because they result in sterile hybrids), and how variation arises (a combination of inheritance and learning; chaffinches tend to breed where they learned their songs, producing local dialects). While Lorenz had no background in geographical work and assumed that signals were arbitrary in structure, Marler argued in 1955 that vocalizations have the structures they do because of their functions. Birds fit his predictions well, particularly in terms of the intended locatability of different signals. Songs (intended to advertise the singer's location to potential mates) contained wide ranges of frequencies with clearly separated notes, difficult-to-locate "seet" alarm calls (intended to be attention-grabbing but not advertise the caller's location to the predator, and to elicit cryptic behavior in receivers) were confined to a narrow band of fairly high frequencies with a continuous structure, and mobbing calls (intended to recruit others to mob a predator) consisted of short, easily locatable "chirps" (Owren & Rendall 2001).

Like birds, humpback whales sing seasonally during pair formation for both intersexual attraction and intrasexual competition. Humpback song was discovered by a Navy engineer listening for submarines with hydrophones in the 1960's and turned over to acoustic biologists who analyzed their structure. The songs are composed of multiple nested components. Like bird song, it is easy for a human to analyze in terms of sequences of discrete units (Payne & McVay 1971). Humpback song is culturally transmitted; each ocean basin has its own song that changes slowly over time as modifications and variants spread, although rapid cultural changes can occur with immigration (Smith et al 2008; Noad et al 2000). Cultural transmission has also been an interest in birdsong research as many songs have an innate basic structure with specifics learned from adults during critical periods using auditory feedback (Hauser 1996).

One common goal is to explain a signal's structure in terms of how it propagates through the environment and what features could be used by receivers to detect and discriminate the signal. These questions can explore why a vocalization uses certain frequencies, why it contains a certain amount of redundancy or why the amount of redundancy might vary with environmental conditions, how much information can be encoded in the signal structure, how much information can be transmitted over different distances as some frequencies attenuate more quickly than others, whether the signal is easy or difficult to locate given its structure, and whether a signal's structure is the result of a tradeoff between information and distance. Marler predicted that forested environments should select for stereotyped calls with simple messages resistant to degradation while open environments allow more complex, graded call structures (Owren & Rendall 2001), as the visual access to context clues in an open environment makes misinterpretation less likely and reduces the amount of selection against intermediate calls that would be ambiguous without context clues. Bioacousticians like R. Haven Wiley have published extensively on the constraints put on the evolution of vocalizations by habitat features and how frequency-dependent attenuation, turbulence, and reverberation affect signal reception (Wiley & Richards 1978, Richards & Wiley 1980, Naguib & Wiley 2001).

Hebets and Anderson (2018) identified a "major paradigm shift" in the early 1990's when communication researchers began to ask questions about receivers: how the form of a signal is determined by its need to be effectively detected and discriminated from the surrounding noise by target receivers, how receivers' biology and psychology influence how they detect signals and respond to them, and how observers can deduce things about receiver biology based on their

responses to signals. Receiver questions include those about perception in general, categorical perception, and how perception affects behavioral responses.

Con Slobodchikoff (2012) discusses the “discourse system”, analogous to systems in physiology, to emphasize the fact that communication depends on the perception of referents and the formation, sending, receiving, and interpreting of signals, all of which depend on organs that are under selection together. An increase in the sophistication of phylogenetic methods used throughout biology in the 1990’s allowed for more informative comparative studies of communication in different species and genera (Hauser 1996, 11). Recent studies have focused on complexity and interactions within communication systems including the signaler, receiver, signaling environment, and relevant aspects of physiology, but specific work in all the previous trends continues. Study of communication systems still includes basic description. Some systems are being assessed with respect to transmission efficacy and receiver detection and discrimination. Fewer are being approached with the intent to understand the message or content of signals with different functions, including semantic content and referential communication.

More recently, humans have been analyzing animal vocalizations and communication systems in terms of information theory and complexity. Like spectrographs, information theory developed out of wartime research for understanding the capacity of communication systems, with the amount of information in a signal depending on how improbable it is to be randomly selected from a set of possible messages. Many fields began thinking in terms of messages and noise (Radick 2007). Complexity is a difficult term to define in bioacoustics, because people are interested in signals that could convey a lot of precise information related to complex social

dynamics. These can't be too "simple" to contain much information, but the most "complex" signal in a traditional sense is that with the most entropy, which would be random noise and not useful for communication (Kershenbaum et al 2017). People study the complexity of signals and communication systems because of how it relates to social complexity and information transfer.

One measure of complexity is the repertoire size of a communication system. A 1997 paper compared alarm call repertoire size with social complexity in three sciurid groups, using information theory to define social complexity as the number of bits needed to describe a social system in terms of the number of demographic roles in social groups, including kinship and time to dispersal. This relationship seemed to hold for *Marmota*, but not for the other genera (Blumetsin & Armitage 1997), probably because alarm call repertoire size is a product of the number of different predators requiring significantly different escape strategies and not a product of sociality. The repertoire size of social signals would be more difficult to determine as it includes multimodal signals, subtle short-range signals, and olfactory signals which humans have difficulty detecting. Many mammal repertoires include graded signal types such that any measure of repertoire size is subject to the individual researcher's propensity for lumping or splitting. Complexity has also been defined in terms of the unpredictability of a sequence of calls or call units. Group size, an aspect of social complexity, explains the individuality of alarm calls in some sciurid groups (Pollard & Blumstein 2012). It stands to reason that a species with a lot of elements and variation in its social and external environment would need a communication system that reflects that variation and flexibility, but ways to quantify what we mean when we talk about social or communicative complexity are still being explored.

Deception is an area of communication that intersects with cognitive ethology. The study of deception became popular during the 60's-70's focus on individual competition, evolutionary game theory, and arms races. Deceptive signals can evolve as morphological structures or fixed action patterns, but the kind of purposeful deception of interest to cognitive ethologists is based on the signaler's beliefs about what the receiver knows. This kind of deception can reveal something about metacognition and theory of mind.

In the wild, some cognitive information can be gleaned by observing of natural events. Psychologists Byrne and Whiten (1985) observed several incidents of deception in wild baboons using gaze cues; in a few of these instances a juvenile encountered an adult occupying a good foraging spot, and after looking around and verifying that nobody was there to call his bluff, he screamed as if the adult was attacking him, prompting his mother to chase the adult away. The kind of deception employed by food-caching corvids also involves looking around to verify that no one is watching before making a cache, moving your cache to a new location, or stealing a cache when its owner is distracted. When ravens determine that they are being watched, they may make a conspicuous false cache to distract potential pilferers (Heinrich 1999).

With any deceptive signals, there is an arms race between signalers and receivers. Receivers are under pressure to become more discerning and skeptical; in turn this puts pressure on the deceptive signals to become more convincing. Receivers can evolve to ignore deceptive displays because of selection pressures on their perceptual systems, or they can use learning and memory to become more discerning over time. In long-lived social species, receivers can remember who is deceptive and become less likely to believe those individuals.

There is also an element of game theory. If everyone in a group is perfectly gullible, one liar would gain a massive fitness advantage by cheating others out of resources. However, liars cannot overtake the entire group, because lying only works when receivers believe the lies, which happens when most of signals the receivers encounter are true. If liars did overtake the entire group, it would no longer be able to provide the benefits of a group to any individual. This is why memory plays an important role in social species, allowing a tit-for-tat strategy for intragroup competition: because most signals are true, receivers believe them at first, but if they catch someone in a lie they can remember who is a liar and not believe them in the future. This is a reason Robin Dunbar (2004) attributes gossip or exchange of social information as a major function of early human language. Wild and captive primates remember if an individual is unreliable in a certain context, if an individual is cooperative or competitive, and what has or has not been seen by whom (Cheney & Seyfarth 1988, Woodruff & Premack 1979, Hare et al 2001).

Observations and experiments involving deceptive communication provide clues about how much the signaler knows about what others are aware of and what information drives the decision to lie or withhold information in a given scenario, providing insight on theory of mind and social cognition. These insights can then be used to more accurately interpret instances of cooperative communication in the same species.

A consistently present yet difficult question is that of semantic content. Marler, Seyfarth, and Cheney may have been the first people to study the meanings of vocalizations since Garner's attempt in the 1890's. While the methods available to humans do not allow direct translation of animal signals into human language as Garner hoped, referential communication can be detected

and quantified. Marler discussed correlations between changes in the signaling environment and changes in vocalizations which may contain information about the signaler and their environment. He also measured receiver responses to determine how much of the potential information they had received. This remains difficult in studies of referential communication because one possible response is to store the information without any immediate outward indication of having received the signal.

Marler described call function as transferring items of information in the form of propositions about the caller and environment. These propositions were not intended as a translation of the call, but as a measure of functional reference. If you observe a prairie dog notice a coyote and make an alarm call after which everyone dives into their burrows, there are several options for interpreting content. The alarm call translated into human language could mean “coyote”, “predator”, “danger”, “flee”, or many other possibilities. It could also have no translation and simply activate a fixed action pattern or trigger an emotion that causes the flee reaction. But based on its function and observed receiver responses, you can say that the alarm call functionally refers to both the predator and the escape strategy. Additional observations and experiments can further clarify the functional referent of the call. The functionally referential call transmits information about the referent, but may or may not cause a symbolic representation of the referent in the receiver’s mind.

Tinbergen’s idea of communication was the signaler activating a response in the receiver. Marler’s interpretation was that if a call elicits a biologically appropriate response, it must have transferred some information; so a call’s function can be described by listing the items of information (propositions about the caller or other referents) contained in the call (Radick 2007).

This is more like the idea of ‘translating’ from one language to another, although Marler was talking purely in terms of functional reference (“do receivers act as if they’ve received this item of information?”). Marler began studying meaning in the 1960’s following his earlier work on call geography and the relationship between structure and function, wanting to know if signals were purposive and what their informational or semantic content was. He called for zoologists to learn from linguists and semioticians when dealing with referential signals (Hauser 1996, 58).

When Seyfarth, Cheney, and Marler published their landmark 1980 research on the functionally referential alarm calls of vervets, they introduced their paper by saying that the study of semantics is a “central but neglected issue” in research of communication under natural conditions. Primatologists in the 60’s noted that vervets used different alarm calls for different predators which elicit different escape responses. Field recordings from Seyfarth et al confirmed that eagle, leopard, and snake calls were acoustically distinct and that each was associated with a distinct escape response (‘look up and/or hide in dense brush’, ‘climb a tree’, and ‘look around on the ground’ respectively). To verify that the calls contained useful semantic information, they used playbacks to test whether the alarm call alone was sufficient to elicit the escape behavior for each predator type. Responses to playbacks often included looking toward the speaker and around for more information as well as the escape strategy appropriate for the alarm call played. Possibly because of the limited repertoire, the authors concluded that these alarm calls were “rudimentary semantic signals”. Within established biological disciplines, claims of linguistic traits tend to be cautious. Almost two decades after these first vervet playbacks, Marc Hauser (a former student of Seyfarth, Cheney, and Marler) described Marler’s primate research as revealing “rudimentary referential properties” and “syntactic potential”. In contrast, a St. Louis

newspaper reporting on Garner's extra-disciplinary work in 1890 readily used the phrase "translate the monkey language" (Radick 2007).

In the same paper, Seyfarth et al started to investigate the influence of learning on the specificity of these signals. Adults were most selective (leopard calls for leopards, eagle calls for martial eagles, snake calls for pythons), while infants gave alarm calls to a variety of stimuli—however, the infants' categories were not entirely inappropriate, just more broad than the adults' (leopard calls for terrestrial mammals, eagle calls for birds and falling leaves, and snake calls for snakes and long objects). This study generated renewed momentum for questions about symbolic reference. Since then, primate communication research especially has been focused more on semantic questions within a paradigm that discusses referential information "encoded" in vocalizations—a model that has been criticized for its implicit assumptions about the nature of information and how it is transferred (Owren & Rendall 2001) but that has been instrumental in the framing of questions about vocal communication that reveal.

Marler's work with vervets showed that nonhuman primates can use signals that function as nouns, but he was skeptical about signals that would function as adjectives. Early in Marler's switch from birds to primates, he said in an overview of animal communication that bee dance language "must be regarded as descriptive, in the same sense in which we apply this to our own language" (Radick 2007). Con Slobodchikoff also demonstrated the existence of nonhuman descriptive signals in the 90's with experimental studies of a wild prairie dog population in which alarm calls varied with physical attributes of approaching humans and could be classified accurately by a discriminant function analysis (Slobodchikoff et al 1991). These descriptive elements were incorporated into the alarm calls regardless of their usefulness in an immediate

sense; changes in calls and relevant escape strategy were made in response to a human firing a gun in the colony in order to be perceived as a threat, but alarm calls still varied depending on purely descriptive aspects of individual humans in the 1991 experiment when all of the humans did nothing but walk through the colony, so there was no difference in escape strategy.

A followup study in 2007 showed that the prairie dogs used different calls in response to the same human wearing two different colors when that human left food in the colony, and different calls when another human entered the colony in the same shirt color before and after firing a gun (Slobodchikoff et al 1991; Frederiksen & Slobodchikoff 2007). Prairie dogs appear to incorporate descriptive elements in their calls that distinguish individual predators even before they know anything about the individual's hunting strategy and an associated escape strategy. These prairie dog studies also helped to dispel the idea that calls lie on a continuum from affective to semantic with responses from physiological to learned. Alarm calls in general have sharp onset, fast rise time, dramatic frequency and amplitude fluctuation, and high-amplitude noisiness; all these features work directly on the mammalian nervous system to cause attention and arousal (Owren & Rendall 2001). The fact that alarm calls are so restricted in structure and consist of features that cause physiological responses in receivers would lead many to assume that it would be futile to look for detailed descriptive terms in alarm calls, but even short bark-like prairie dog alarm calls can contain semantic information unrelated to the acoustic startle response or to predator-specific escape strategies.

Later experiments in Marler's career also showed the variation in possible meanings of alarm calls. In the 1990's he studied referential calls in captive chickens, experimentally changing the stimuli for food and alarm calls to figure out what features of a referent actually

elicit the call. Manipulating the apparent referents of alarm calls in captivity allowed Evans and Marler (1995) to determine that chickens' aerial and terrestrial alarm calls referred to the location of the predator in terms of its height above the ground, not to the species of predator type. This kind of information would not have been available in a normal setting, as predator type and location are related, but the captive scenario allowed experimenters to project images of terrestrial predators above the ground. After observation in the evolutionary environment and experiments with normal referents, experiments that systematically manipulate features of referent stimuli can narrow down the conclusions about functional reference and allow us to make more educated hypotheses about what a signal means to signalers and receivers.

The Language Debate

> *To deny animals language because it is unintelligible to us would be as absurd as for the crows to maintain that their croaking is the only rational speech, and that we are devoid of reason because we do not understand it; or for the inhabitants of Attica to claim that theirs is the only language, and that all who do not speak it are devoid of reason.*
>
> –Porphyry, 3rd century, quoted in Evans 1891

Studies of animal communication, especially those dealing with semantic meaning in vocalizations, always occur in some position relative to the "language debate". Language has long been a mainstay of the notion that humans are unique among animals. 'Only humans have language' has persisted long after the demise of ideas like 'only humans use tools' and 'only humans have minds'. As Marc Hauser notes, "we tend to be much more possessive about some traits than others" (Hauser 1996, 31). Humans want to believe that they are the most intelligent or that their cognition is the most complex, and because language has been equated to

intelligence, it brings out that possessiveness in humans. The traits humans consider most important are based on their own cultural biases, not what is adaptive for a species' particular environment. A desire to be unique has led many philosophers, linguists, psychologists, biologists, philologists, and anthropologists to explicitly or implicitly follow Friedrich Max Müller's 1861 declaration that "the one great barrier between the brute and the man is *Language.* Man speaks, and no brute has ever uttered a word. Language is our Rubicon, and no brute will dare to cross it" (Piattelli 2016).

The question of humans being uniquely linguistic and uniquely intelligent permeated discussions of language origins. Müller's series of lectures on the comparative philology in the 1860's took place about a decade before Darwin's *The Descent of Man* and claimed linguistic roots were equivalent to concepts, and because reason was conceptual, language and reason were aspects of one phenomenon (Radick 2007). The argument that language and reason were the same or that one was not possible without the other continued with various explanations given throughout the 19th century. Earlier, this idea was extended to "if you don't have language, you must not have cognition"—even nonverbal humans were said to be unable to think. Even so, Müller's contemporaries did point out that his line of thought would lead to the conclusions that infants are not human, deaf-mutes cannot think, and a person who thinks of something while forgetting the word for it is not thinking of it at all (Radick 2007).

Victorian British philologists generally accepted the premise that only humans had general ideas or concepts, and that animals were only capable of thinking about specific objects. Mental faculties in general were seen to mark an "impassable barrier between humans and other

animals" (Piattelli 2016). Müller believed that concepts were the same as roots in language, so that if animals have no concepts, they must have no language and vice versa (Radick 2007, 22). Because of how he viewed words as equivalent to ideas, he said the uniqueness of human language was an outward expression of a unique ability to deal with general concepts.

Müller defended his ideas to the point of absurdity, invoking a catastrophist account of language formation in which early humans somehow obtained a genetic feature that caused the formation of roots and then vanished. This vanished-instinct theory was proposed as an alternative to the onomatopoeic ("bow-wow") and interjectional ("pooh-pooh") theories of language origins on the basis that they did not explain the emergence of arbitrary roots. Uniformitarianism had been the intellectual standard since Charles Lyell's *Principles of Geology* in the early 1830's. Across disciplines there was a preference for explanations involving gradual change and a resistance to explanations of the past that invoked processes not known to be acting in the present (Radick 2007, 26). The "temporary creative faculty" sounded ridiculous in a post-Lyell intellectual environment, especially after Darwin's promotion of uniformitarianism with respect to the gradual acquisition of biological traits and abilities: "Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation" (Darwin 1859). Darwin also criticized Robert Chambers for including a similar catastrophist hypothesis about language origins, one that relied on the past appearance of an adaptive force with no evidence besides the existence of thing it was supposed to have caused, in *Vestiges of the Natural History of Creation* (1844).

Hensleigh Wedgwood, philologist, etymology expert, and Darwin's cousin, wrote a paper on onomatopoeia in 1845 and cited imitation as the origin of language. For Wedgwood, "bow-wow" and "pooh-pooh" were both forms of imitation: onomatopoeia was imitation of the sound of a referent and interjection was the voluntary imitation of an emotional vocalization which would normally be spontaneous. This seen in the wild: when birds make false alarm calls in order to steal food from the birds who hear the alarm and flee (Moller 2010), they're voluntarily imitating a vocalization that likely evolved from a spontaneous display of fear at the approach of a predator. When chimpanzees scream in order to solicit help in a fight and voluntarily exaggerate the screams depending on the audience (Slocombe & Zuberbühler 2007), they're imitating a vocalization that would normally be spontaneous in order to influence receivers by making them believe something about the signaler's mental state. Wedgwood's theory was that early humans made spontaneous vocalizations in response to some emotion and then associated the sounds with the corresponding mental states, and then they could make those sounds on purpose to refer to the mental states.

Whether or not language roots are descended from interjections, it is more probable that this process existed early in human evolution (and persists in words like "ow" and "brr") than Wedgwood's ideas about onomatopoeia. He said that the only way for pre-linguistic humans to refer to something like a dog was to imitate it ("bow-wow") because that's how modern humans without a shared language would do it, but he was lacking the ethological perspective to realize that in "the wild" one would only refer to a dog for some reason or to elicit some response, and for a non-linguistic or pre-linguistic species it would be most important to convey the reason, not the description of the dog. The most important thing to communicate is what should be done

about the dog—hunt it, fight it, flee from it, pay attention to it, etc. Specificity of species can come later. In nonhuman animals with species-specific alarm calls such as vervets and prairie dogs, the way their alarm calls vary between referents isn't onomatopoetic; a vervet's hawk call doesn't resemble a hawk, and a prairie dog's alarm call variants that describe an individual human based on traits like height and shirt color don't resemble things like tallness or blueness (Slobodchikoff, Paseka, & Verdolin 2009). When Wedgwood was writing, British scientists were unaware of those examples and philologists were not interested in extant nonhuman animals—they only studied modern humans and made inferences about their ancestors. Müller rejected comparative methods using nonhumans and ontogeny-based investigations of human babies; he refused to argue "in the nursery or the menagerie" while George John Romanes looked in those places for clues about the "primitive" condition (Radick 2007).

An important feature of language is arbitrary signs which are structurally independent of their meanings. The origin of arbitrariness was not explained by either of the two main theories on language origins at the time. How did onomatopoeic or interjectional vocalizations become arbitrary signals, or signs that were associated with meanings without resembling their referents, such as words or roots? Müller called onomatopoeia "sterile" and interjections "the outskirts of real language" (Piattelli 2016), believing it was impossible for these vocalizations to be the origins of words. Without a theory for how an imitative signal could change form and remain associated with a meaning, he did not think it was possible to get arbitrary roots from non-arbitrary precursors— "no process of natural selection will ever distill significant words out of the notes of birds or the cries of beasts"—even after Wedgwood brought up how meanings can

be extended and associations formed through analogy and metaphor (Piattelli 2016). Because Müller wanted linguistic roots to be unique to humans, and he knew that imitation was found in other species, he automatically argued against the imitative theory. To Müller, Wedgwood's imitation theory "posed a threat to the alleged uniqueness of human language" (Piattelli 2016). Imitation could only apply to specific referents, and Müller thought the first words had to stand for (and be equivalent to) general ideas. He invented the vanished-instinct theory to explain how humans obtained the ability to express general ideas as sounds in the form of roots, giving no account of how this creative faculty came about, how it was lost, or why he thought it could never happen to another species. Only after the publication of *The Descent of Man* in 1871 did Müller acknowledge that the first human utterances must have been interjections and imitations, and that one must ask how those vocalizations led to roots.

Wedgwood's way of defending human uniqueness was to state that imitation was based on the perception of resemblance and that only humans were able to recognize resemblances between different objects. How Wedgwood thought nonhuman animals could survive without the ability to recognize resemblances and sort objects into categories based on those resemblances is unclear, but philologists must have been spending too much time indoors if they believed only humans could form important categories like "predator" and "edible" based on objects having something in common. As William Dwight Whitney said in his critique of Müller, "it is a necessary attribute" for anything one would normally call intelligence (Whitney 1874).

Darwin agreed with Wedgwood on the imitative origins of language in *The Descent of Man*, though rejecting his cousin's ideas about the uniqueness of imitation and the idea that

language first developed in modern humans. While Darwin said that language developed along with humans themselves, Wedgwood in 1872 presented a scenario in which our ancestors began using imitative signs only after already becoming otherwise identical to modern humans, holding onto his previous notion that early language arose in humans like ourselves (Piattelli 2016).

In the 1880's, anthropologists stepped away from the idea that the origins of human language could be found in extant nonhuman apes and began focusing on fossils. They debated about the presence of language in different hominids based on anatomical features specific to modern language including the presence of genial tubes and whether skulls contained room for a well-developed Broca's area (Radick 2006, 180). By the 1910's anthropologists realized that other primates had been following their own evolutionary trajectories rather than sitting on a ladder unfolding toward the human condition, so they were more than stages humans went through in the past (Radick 2007). Like the linguists and philologists, anthropologists interested in the origins of language generally lost interest in studying other extant species.

Meanwhile, the fields that did study extant nonhuman animals were moving toward a proto-behaviorist framework. Certain kinds of intelligence remained caught up in the uniqueness battle and fueled skepticism about the reasoning abilities of non-linguistic animals. Psychologist Conwy Lloyd Morgan, who was active from the 1880's to 1930's, often talked about positivism. He expressed the view that one should not assume one way or the other about whether an apparently clever behavior was the result of reason and planning or a less intelligent mechanism like instinct or trial-and-error learning. Yet in his letters with Müller, he readily accepted the idea that language and abstract thought were inseparable, thus any action taken by a non-linguistic animal must not be the result of methodical planning (Radick 2007, 77). Morgan had no way to

detect reason without language besides behavior, which he already rejected; effectively claiming that the only permissible evidence of reason is self-reporting through language. He also failed to define language in terms of its own characteristics and ended up with a circular model: ‘language is something that includes symbols for concepts; concepts are something that cannot exist without language; and reason is something that cannot exist without concepts’. He built a set of circular definitions such that anyone mentally handling isolated abstract concepts without language would be defined as ‘not reasoning’.

Morgan was not the only psychologist to say that it must be impossible to think about abstract concepts without language because it was hard for him to imagine doing so. This is surprising because in the midst of the language debate, psychologists forgot how humans actually think. All humans must think about concepts without language—some more than others, as with autism which leans toward visual and spatial thought (Grandin 2005), but everyone has found themselves thinking of something (an object, idea, concept, or relation between concepts) without remembering the word for it. If it were impossible to think of a concept without a linguistic symbol, no one could ever think about something for which they have forgotten the word. Additionally, if word and concept were so tightly bound, a human would never be able to learn a word and match it to a concept, since they would not have a concept to match to the word without already knowing the word. Unless psychologists like Morgan were somehow born with immense vocabularies, they apparently forgot how they learned their own first languages and how they thought and learned words for concepts when their vocabularies were small.

In 1892, leading up to the behaviorist turn in psychology, Morgan wrote what became known as Morgan’s Canon: “in no case is an animal activity to be interpreted as the outcome of

the exercise of a higher psychical faculty, if it can be fairly interpreted as the outcome of the exercise of one which stands lower in the psychological scale" (Radick 2007). This was an attempt at simplification along the lines of Occam's Razor, but led to some overly complicated conclusions, like the idea that it was easier to evolve a predetermined internal flowchart with instinctual responses pre-coded for a huge number of possible situations rather than simply evolving the ability to use memory and mental representations to figure out what to do in a new situation through reasoning. Despite its absurdity in the context of long-lived species with variable environments requiring flexible behavior, Morgan's Canon was adopted so widely into the dominant paradigms of psychology and biology that historians considered it inevitable. Morgan's Canon was never applied to humans, but it was intended to be used for analyzing the actions of all nonhuman animals, regardless of their environments and the evolutionary pressures on their intellect; so the application of the Canon served the interests of the uniqueness-defense team. As Whitney put it in 1874, "the dog may have as good a right to complain of Müller for putting him and the oyster into the same class of "animals" from whom man must be made out essentially different, as Müller to complain of Darwin for putting man and the dog together".

While Morgan himself was in theory not committed to the uniqueness of human language or reason—in 1893 he said that "I shall not be the least ashamed of myself if I change this view before the close of the present year. And the distinction between intelligence and reason will remain precisely the same if [nonhuman] animals are proved to be rational beings the day after tomorrow"—he operated with the tacit assumption of uniqueness and used the words 'language', 'reason', and 'human' as if they were synonymous (Radick 2007). This led others, especially those with a pre-existing bias in favor of uniqueness, to embrace the same assumptions. In the

1880's and '90's, the popularity of Morgan's canon overshadowed the kind of comparative psychology advocated by George John Romanes. While Romanes focused on mental and cerebral continuity, those who overzealously applied Morgan's Canon reinforced Müller's Rubicon and the appearance of a wide gap between humans and everyone else.

William Dwight Whitney's 1874 response to Müller included some arguments that apply as much to Morgan. Speech may be an important avenue to determining the specifics of a human's mental state, but it is not necessary or sufficient—even when dealing with humans, one should not trust their self-reporting without using other cues.

> We believe that the horse sees green, and tastes water, and feels pain, as confidently, and on nearly the same grounds, as we believe that our neighbor does the same. We are satisfied that we appreciate the feeling that makes puppies and kittens play, or the dog rub itself against its master, or look affectionately up into his face and wag its tail. It may be very unphilosophical; but it is part of the same common-sense philosophy which makes us believe in our own existence, and in that of beings and things external to ourselves, and of which every metaphysician that says "I" and "we" and "you" and "they" virtually acknowledges the truth, however firmly he may persuade himself that he has assurance of nothing in the universe save his own states of mind, if even of those. We have, it is true, one additional source of knowledge respecting our fellow-men, namely, their speech … but it is not the only source, nor is it infallible; it requires to be both supplemented and controlled by that same observation of conduct under conditions which is all we have to rely upon in the lower animals.

Whitney also pointed out that speech is fundamentally driven by the need to communicate, not for any individual's benefit for reasoning in isolation. Another call for consistency in the attribution of mental states based on expressions and behavior came from F. Julia Wedgwood in an 1873 letter to Darwin about Müller, based on a Darwinian principle: "when signs have been ascertained to denote things in one place they shall be supposed to denote them in another till proof is shewn to the contrary" (Wedgwood 1873).

Many of the objections to Morgan and Müller which would come naturally to a present-day reader were covered in an 1891 article by E. P. Evans. These include the fact that concepts must have preceded roots, that Müller was just guessing that no animal signals were about general concepts, that speech may be helpful to mental operations and complex reasoning but is not a requirement for it, that human babies cannot speak any more than dogs can, and that many animals can clearly generalize. He said that philologists could never discover the origins of language as long as they were unwilling to go beyond roots. In the philologists' paradigm, roots were "assumed to be ultimate and unanalyzable elements, like the purely hypothetical particles which the physicist calls atoms". Comparative psychology, on the other hand, can investigate language origins. Evans pointed to Broca's aphasia as evidence that language was separate from reason, as a lesion in the third frontal convolution of the left hemisphere can eliminate speech but not reason; he also cited research showing that brain injuries can disrupt birdsong, causing wrong notes and muddled syntax. Darwin also read the aphasia research coming out in the 1860's and concluded that it was proof that rationality and language were separate, so they did not have to emerge together in a single catastrophic Müllerian leap—and of course it also showed that one could have rationality without language (Radick 2007).

Besides repeating pre-Boasian ideas about the existence of 'primitive' modern humans and Darwin's inexplicable claim that wolves cannot bark, Evans sounds much like a person from today would if asked to respond to Müller's claims about reason and language. One exception, at least in the fields of linguistics and animal communication, is that Evans is willing to call "language" anything that gives others information about what the signaler is thinking: "No one asserts that [exclamations] are words in the strict sense of the term; all that is claimed for them is

that they express thoughts and feelings or reveal states of mind, and may be regarded as language". He also quoted an ancient opinion from Porphyry, who said it would be "absurd" to deny that animals have language when they can express different emotions using expressive displays. While this remains common as a layman's definition of language, linguists and communication researchers would not consider a species that can only express emotions or affective states to have a language; definitions vary but they usually require the ability to functionally refer to external objects and events and some kind of combinatorial syntax. Even so, it is more productive to assume that a species has some language to discover than it is to assume only humans have language and therefore it would be fruitless to make any attempt at studying animal communication at all. Evans is also accurate in his comparisons to the Müller and Morgan camp, who did not deny animals language because of any diagnostic criteria, but because they were not human. "The Greeks called beasts speechless creatures just as they called foreigners tongueless, meaning thereby persons whose language was unintelligible to them; and the epithet was no more appropriate in the former case than in the latter" (Evans 1891).

Between the experimental, behaviorist turn in the 1900's-10's and the ethological turn in the 1930's-40's, psychologists underestimated animals' ability to use ideas and concepts, and language questions disappeared for a while. Some research claimed to discover "words" in a broad sense, but not "language". The artificial, laboratory-based paradigm influenced ape-language studies which consisted of attempting to teach human vocal languages to captive nonhuman apes were unproductive.

In the late 1950's and '60's, anthropological linguist Charles Hockett attempted to define language (in contrast to general communication, which he said was any behavior by which one organism triggers another) using a list of design features supposedly found in all human languages such that no other species had a communication system that included all of these language features. Hockett's list ranged from 7 to 16 design features at different times, but in every iteration of the list, humans were able to claim the full set of features and other species' communication systems were described as different incomplete combinations of those features.

Hockett's fixation on humans led him to value traits not because of how useful or adaptive they were, but simply because they appeared in most human communication. His criteria even excluded several forms of human language such as sign language, writing, and recordings of speech because of his 'vocal-auditory channel' and 'rapid fading' requirements. His discreteness criterion, while useful for productivity, would also exclude human speech if studied objectively as it is emitted as a continuous signal and only becomes discrete on the receiver end due to categorical perceptive mechanisms.

Hockett claimed he wasn't interested in human uniqueness and that if any other species displayed all of his design features, he would admit that they had language, but his choice of several features on the list was obviously driven by nothing more than their presence in human communication. Some of his features were correlated and should never have been included on the same list; for example, discreteness and productivity: as far as we know, productivity can only come from combining discrete units in different ways (Pinker 1994); the vocal-auditory channel, rapid fading, broadcast transmission, and directional reception are all related to sound, which Hockett only chose because he was using spoken language as a model. His explanation for

the language gap was competitive exclusion: any species with language or proto-language that was alive at the same time as early humans would have been in fierce competition with them, and the humans would have outcompeted them because of their linguistic advantage. This is primarily why Hockett did not expect to find what he considered true language in other great apes, and why he thought humans were "lonesome" in their abilities (Radick 2007).

A few of Hockett's language features are relevant for explaining why human language is so powerful. Possibly the most important is productivity, or the ability to say new things; in humans this is a result of a combinatorial structure that makes the repertoire size practically infinite. Arbitrariness allows for the specialization and productivity of language. Displacement, both in the sense of referring to things distant from the signaler in time and space and distance between the signal and the response, is useful for group coordination and planning. Cultural transmission shows that the communication system is learned and subject to cultural evolution, which is faster than genetic evolution and allows groups to keep up with rapid changes in the environment. The last important feature is semanticity: signals must be symbols associated with referents if they are to function by eliciting mental representations.

The idea that language can be defined through a list of design features persisted after Hockett and remains a ubiquitous presence in discussions of animal communication systems and animal language. While it is biologically meaningless to hold up one species as the gold standard to measure every other species against, it is important to analyze communication systems in terms of what kinds of things they can do and why their evolutionary environments resulted in the need for some abilities and not others.

Even without an emotional investment in human uniqueness, 19th century philologists assumed that human language was unique because they were embedded in a paradigm that fostered that assumption and did not encourage the study of nonhuman animals. Wedgwood's ignorance of extant nonhuman animals showed itself when he talked about imitation, recognition of resemblance, and "appreciating each other's motives". The way he talked about early language also revealed that his world of possible questions was different from that of an ethologist—he referred to early language as "using imitative signs for the purpose of bringing absent things to the thoughts of another mind" (Piattelli 2016). After the rise of behaviorist psychology, questions about unobservable thoughts were replaced with questions about observable behavior. With the adaptive focus of ethology, questions about changing another's thoughts became questions about changing another's behavior. This can be done through bringing things to the thoughts of another mind, but since only the resulting change in the other's behavior can affect the signaler's fitness, the part of the process that is under selection is the ability to affect behavior). Communication was defined as what has evolved because of its ability to affect receiver behavior in a way that increases the sender's fitness. It was not until the emergence of cognitive ethology in the 1970's that 'communication as a way to bring thoughts to another's mind' reappeared as a possible conceptual framework for researchers thinking about communication, although thoughts are impossible to observe and behavior remains the easiest and often the only way to observe the effects of communication.

1970's ethologists viewed the origins of communicative signals in terms of gradual formalization of a precursor with some preadaptive capacity for being informative (Smith 1977, 313). The precursor could be anything that happens to make socially useful information available

to others; if the ability to share this information improves fitness, selection can then act on the precursor to make it increasingly specialized to provide information to others. The formalization process can occur through genetic or cultural evolution, and as a signal becomes more specialized, the loss of resemblance to its past function would be gradual. The arbitrariness that confounded Müller is now explainable by a theory of branching evolution. Gradual changes as a result of selection for more informativeness can cause a signal to become increasingly arbitrary with respect to its referent. One could not pinpoint exactly when a signal switched from arbitrary to non-arbitrary, but the relationship of a signal to its referent can become less obvious over time until a researcher encountering it in the wild would classify it as arbitrary.

The 1970's also ushered in a sociobiological turn in behavior and psychology which replaced an older tendency for social scientists to ignore the relevance of evolutionary history on human social phenomena. Hockett coined the word "sociobiology" (Radick 2007), but the field was largely popularized after the 1975 publication of *Sociobiology: The New Synthesis* by E. O. Wilson, whose history studying insects gave him an evolutionary perspective on social organization. With an ethological approach to social behavior and attention to natural selection at the group level as it applies to humans and other social species (instead of a Dawkins-like approach which only discusses the effects of kin selection), language evolution was brought to the interactions between genetics and learning. Sociobiology closed the gap between humans and other species in terms of behavior, and while linguistic communication is a behavior, its usage is still mostly studied in terms of voluntary communication decisions by individual humans influenced by learning and culture. Its structure, on the other hand, is more often discussed in terms of its evolutionary history and genetic components.

Modern ideas of language origins owe much to sociobiology. Newer accounts of the history of language tend to be more comparative, unlike those of Müller and Wedgwood, but remain primate-centered. A focus on human anatomy and how humans evolved language may obscure other possible origins of language and the structures and pressures that could lead to linguistic communication in non-primates. Those attempting to clarify the origins of language are also necessarily subscribing to some definition of language, even if it remains unstated.

Between the 1860's and the end of the next century, linguists ignored questions about language origins because there was too much speculation. When these questions came back into vogue, linguists continued to struggle with finding a definition of language because they were unwilling to look outside of primates for clues. Continuing debates include language definitions, which features were preadaptations for language, relative contributions of biological evolution, cultural transmission, and individual learning to the development of language, and mechanisms of linguistic development that can be explored in computer simulations (Christiansen & Kirby 2003).

Linguists and anthropologists maintain some obvious blind spots with regard to animal communication, ethological questions, and anything outside of primates. They acknowledge that human communication is uniquely complex among primates, and that the reason for this must have to do with differences in selection pressures and the presence of some preadaptations, but they consistently fail to ask about what communication looks like in non-primates that experience similar selection pressures. It is possible that certain pressures as well as certain preadaptations found in primates are necessary for language evolution, but linguists can only

speculate about this if they continue to restrict themselves to primates. Robbins Burling (1993) demonstrated this lack of familiarity with animal communication research outside of the human lineage by saying that there is no way to detect discrete perception of sounds (although researchers working with animals and infants regularly use methods like habituation-dishabituation tests to judge whether a participant perceives two stimuli as ‘same’ or ‘different’) and ignoring the existence of discrete systems in non-primates. He also neglects the subjective and cognitive aspects of ethology by failing to realize how discreteness in a vocalization system is defined by perceptual categories and accusing researchers studying voluntary communication of searching for language rather than being interested in the cognitive questions one can answer by observing when and how voluntary signals are used.

Burling pointed out that most primate communication is of the same kind as human nonverbal communication, and that the roots of human language should be explored through the cognitive abilities of other primates instead of their communication abilities. There is a general consensus that neural adaptations necessary for language include an increased ability to deal with hierarchically organized, temporally ordered concepts, but Burling sees this as a part of language rather than a preadaptation or something that coevolved with syntactical communication. Burling also exemplifies a trend of focusing on structure at the expense of evolutionary considerations—he quotes Derek Bickerton calling a focus on communication a “hangup” in the study of language origins, despite selection on language acting on its ability to function as a communication system. This leads linguists to imply that any sufficiently ‘smart’ animal (in terms of symbolic hierarchal organization in thinking) will develop language regardless of the

presence or absence of the necessary pressures on communication (a complex social environment and the need to communicate specific information within a group).

In the 1990's, anthropologists debated about how recent 'true language' was as a development in humans. As spoken language cannot be detected in the archeological record, they tried to use artifacts and anatomy to determine whether language was present. There were arguments over how to define language and "whether it should be defined in such a way as to emphasize the differences between modern human and ape vocal communication or to recognize their similarities" (Aiello & Dunbar 1993). A linear relationship was found between logarithms of group size and relative neocortex size in catarrhine species without a fission-fusion social system as well as a linear relationship between group size and time spent grooming, and the resulting model applied to fossil hominids implied that group sizes were large enough to require grooming multiple individuals at once by the second half of the Middle Pleistocene. These large group sizes can be maintained through contact calls that function as vocal grooming. Dunbar argues that language evolved from vocal grooming and continues to serve the same purpose. If contemporary humans had no language or vocal grooming, they would have to spend 30-45% of the day on social grooming to maintain group cohesion using the group sizes predicted by neocortex volume (Aiello & Dunbar 1993).

The social origins of language are comprehensible only from a group-selection perspective, as the main pressures that favor large group sizes in primates are predation and inter-group competition (although cooperative hunting may have been a factor for early humans). Many people believe language is useful primarily for accomplishing technical tasks and sharing information about the outside world. Robin Dunbar (2004) found that many people consider

gossip or social topics to be an idle side effect of language rather than its main purpose, but over half of sampled human conversations were about social topics. Additionally, many species that are not considered to have proper language, such as wolves, can coordinate complex activities like group hunting of difficult prey with division of labor (Haber & Holleman 2013). While wolves may have more information in their short-distance vocalizations than we've discovered, it is more likely that they don't need to meet up before a hunt and use language to assign tasks beforehand. Experience and observation of previous hunts will tell wolves which pack member is the best at a given task, and close observations of packmates while hunting, combined with knowledge gained from watching previous hunts, can tell them where they will be most useful at any given moment.

It appears that non-linguistic learning and observation are sufficient to coordinate complex activity in a group, but what holds the group together in the first place? In primates, group size is limited by the amount of available time for social grooming; grooming triggers an endorphin response which mediates relationship quality, and a social group is maintained by continuous maintenance of individual social networks. Dunbar (2017) suggests that laughter was an early form of vocal grooming, a form of social chorus that effectively grooms everyone involved by triggering an endorphin response. A later form was singing, a form of chorusing that involved breath control and long exhalations which are also necessary for speech. In 1872 (*Expression of the Emotions in Man and Animals*) Darwin speculated that human language may have evolved from singing, like modern gibbons for courtship purposes including emotional expression and later leading to words for complex emotions. Wilson (2012) thinks that music grew out of language instead of predating it, but other species that we consider nonlinguistic use

what we call songs to express emotion, create group cohesion, and attract mates; humans probably had culturally transmitted songs before anything like modern language. Dunbar's theory is that wordless singing functioned as a group chorus which strengthened social bonds and provided a template for vocal conversation. In this way, Dunbar suggests, language evolved in humans primarily as a way to increase the number of individuals one could groom at a time, allowing the formation of larger groups that could survive on the open savannah.

One alternative to the vocal grooming hypothesis, aside from the common idea that human language resulted from increasing pressures on the semantic content and specificity of vocal calls, is the hypothesis that humans first developed linguistic signs in the form of manual gesture and later recruited the vocal apparatus for linguistic communication. Michael Corballis (2003) forwarded this argument because the Broca's area homologue in monkeys is not related to vocal communication, but deals with manual movements and mirror neurons; this also explains why the only species with handedness is the one in which the Broca's area was lateralized.

A recurring theme in the language debate is the claim that all nonhuman animal communication is emotional, while human communication is semantic. This dichotomy is framed in various ways including 'articulate vs. inarticulate' and 'affective vs. referential', but it crops up in discussions of language throughout several centuries. Darwin (1871) distinguished between articulate and inarticulate language and said that the former was unique to humans. He used 'articulate' to mean communicating about ideas and 'inarticulate' to mean expressing emotions. In 1873 Müller made a distinction between "emotional language", which he said was shared by all animals, and "rational language" which was unique to humans; in 1948, Alfred Kroeber would repeat the same idea: that all animal communication as well as the 'inarticulate

utterances' of humans could express subjective conditions, but only human language could express objective information (Radick 2007). Müller at first tried to use this 'difference of kind' as evidence that rational language did not evolve from emotional language (even though species and traits were known to evolve from other species or traits of 'different kinds') and must have had some catastrophist origin, although he later admitted that language probably originated in emotional interjections (Radick 2007). Evans (1891) pointed out that "thoughts and feelings are inextricably interblended", so there is no sharp categorical delineation between the 'language of thought' and the 'language of emotion', but he implicitly maintained the idea that all symbols fall somewhere along one axis from 100% emotional to 100% semantic.

Before 1980, even those who were not skeptical about the existence of nonhuman sematic signals assumed that alarm calls could not be semantic because they were emotional (Hauser 1996, 58). Alarm calls occur in dangerous contexts with signalers in heightened emotional states. If one's mental image of call type variation lies on a single axis from emotional to semantic, then highly emotional alarm calls must not be semantic at all; this assumption was held by linguists in the 1970's as well as ethologists like W. John Smith. 'Animal communication' as a whole was presumed to communicate about emotions, motivational states, and arousal levels, but not external objects; species that used different alarm calls for different predators were assumed to be referring to different levels of urgency. Smith (1977) put a lot of emphasis on context to explain different escape strategies; he assumed a "leopard alarm call" did not mean "leopard" but merely expressed fear, and receivers would have to look around for context clues to figure out which escape strategy to use.

Seyfarth, Cheney, and Marler showed that alarm call structure contained information about predator type and not just arousal, as a sighting of any predator type could be more or less urgent, but alarm call types correspond to predator types and not the amount of danger posed by a particular predator; and that additional context cues were not required to elicit the correct escape response for a particular predator type. Urgency and semantic content do not compete for space within a call but can be expressed simultaneously. This should have been obvious to humans, who are able to include varying levels of arousal into the same signal without changing the amount of semantic content. A hiker who calmly states "there's a bear in the trail" after noticing a bear a long distance ahead could also yell "THERE'S A BEAR IN THE TRAIL!" with a high level of arousal and urgency after stumbling upon the bear at close distance; the added emotional content would not remove any of the semantic content from the vocalization.

Clearly, arousal and semantics should be viewed as two axes rather than one continuum, but the continuum idea survived implicitly and continues to appear in discussions of semantic signals. As recently as 2015, Wacewicz and Żywiczyński rejected alarm calls as a useful area of study because they are mostly under limbic control rather than neocortical, implying that if a signal is emotional it must not be semantic. Wolf howling is still commonly described as emotional but not necessarily semantic; often with the implication that it would be futile to look for semantic content in howls because we already know they contain emotional messages. Systems of calls in various species have also been divided into those that incorporate labels and those that communicate levels of response urgency, but several species including primates and suricates are known to have both reference and urgency in their calls (Manser 2001).

Grace De Laguna, an anthropologist and psychologist, posited a more behavioristic and evolutionary approach to the 'emotions vs. ideas' problem. In her 1927 book, De Laguna said that there was no reason to talk about communication in terms of its content at all when one could describe it in terms of its evolutionary 'purpose'. Radick describes this turn away from mentalistic explanations: "Previous thinkers had been too much inside the heads of vocalizing animals and speaking humans. Interpreting the former as expressing emotions, and the latter as communicating ideas, they had stuck themselves with the impossible task of explaining how emotional expressions had evolved into symbolic language." Rather than asking what vocalizations are or even what they mean, De Laguna asked what vocalizations do because that is what selection acts on; and what vocalizations do is coordinate social action. There is no apparent gap between humans and other animals if everyone's vocalizations are only analyzed in terms of what they do—but questions about how they do those things (such as by eliciting instinctive responses or by causing mental representations that allow receivers to make onscious decisions about how to respond) and what it is like to the animals in question still rely on explanations of signal structure, information, meaning, content, and semantics.

To this day, analytical linguists who study syntax within human language remain largely uninterested in the adaptiveness of language and the evolutionary pressures that led to it. Syntax itself is difficult to study in most species, despite its importance in discovering combinatorial structures that could indicate a productive language, because the unit of analysis is usually the call or song. This is usually the case because humans have not discovered the meaningful units of organization for most species (Hauser 1996, 3-12). According to Marc Hauser, "there can be

no formal study of syntax without first studying call meaning", and many attempts to identify syntactical structures are lacking an investigation of call meaning (Hauser 1996, 12).

On the other hand, studies of call meaning tend to make the opposite mistake: we can show a statistically significant difference between calls made in different contexts, and a computer can assign a call to a context based on prior data, but parts of the call are not yet 'translatable' into distinct meaningful units. Con Slobodchikoff's descriptive prairie dog calls contained information about color in that there was a difference between calls about humans in blue and yellow shirts (with the size of the human held constant). A discriminant function analysis found the fundamental frequency, ascending slope, and time of ascending slope were used to distinguish shirt colors in the chevron-shaped alarm calls, meaning that while the alarm calls are restricted to short continuous bursts that sweep up and then down, modifications to this basic structure can be used to describe individual predators (Placer et al 2006). This project did recruit human language recognition software to detect units and sequences of units related to different predator types, but they have not followed up on this research since the 2000's. Our understanding of the relevant acoustic and semantic units in human language is what allows us to describe our own syntax and grammar so completely. Study of syntax in other species with continuous vocalizations will require methods to identify the basic units of analysis; only then can syntax be described in ways that allow syntactical communication in other species to be compared to humans in terms of genetics, learning, ontogeny, and semanticity.

Ultimately, the meaning of the language debate boils down to the definition of language and the question of whether it is useful to define one kind of communication or set of

communication systems as “language” at all. The efficacy of the language debate comes into question when confronted with the myriad definitions of language and their origins.

When asked to define language, most people would say that it consists of anything that conveys semantic meaning, but there has also been a consistent argument that a language must have a grammatical structure. In the 1890’s, Morgan said that if an animal word is a brick, animal languages are heaps of bricks, while proper human language is an organized structure of bricks (Radick 2007). Others are more concerned with content. Evans (1891) quoted psychologist Wilhelm Wundt: “If psychologists of today, ignoring all that an animal can express through gestures and sounds, limit the possession of language to human beings, such a conclusion is scarcely less absurd than that of many philosophers of antiquity who regarded the languages of barbarous nations as animal cries”—Wundt defined language in terms of what content it can express rather than how it expresses content, how it’s structured, how it evolves, or how it develops in an organism. Wedgwood described the purpose of early language as “bringing absent things to the thoughts of another mind” (Piattelli 2016). Marler also considered human language less categorically different from animal communication, but said in the 1950’s that the “human-animal divide” was nothing but variation in the complexity of the information transmitted in signals. He put alarm calls, songs, and sentences on one graded continuum from least to most complex (Radick 2007). Marler’s idea of what makes a language was based on information transfer. While he noted that human language possessed unique features, he didn’t use those features to define language; he said “the voice of the chaffinch can surely be said to serve as language” because of its functionally referential properties (Radick 2007).

In 1948, Alfred Kroeber, a Boasian who saw language as a superorganic phenomenon subject to different laws than evolutionary traits, defined it as “a system of audible symbols able to communicate objective facts”. He used ‘subjective’ to refer to emotions, affects, and internal states and ‘objective’ to mean information about the external world. He said that nonlinguistic human vocalizations and all animal vocalizations were outside of language proper and that true language had animal origins but it was of a different kind, not just a different degree (Radick 2007). In some ways this is a reflection of the ‘emotional vs. semantic’ question, but it also suggests an artificial distinction between referents that are external or internal to the organism.

Anthropologist Edward Sapir called language “a purely human and non-instinctive method of communicating ideas, emotions, and desires by means of a system of voluntarily produced symbols” in 1921—apparently he thought a communication system fitting the rest of his definition would only count if found in humans. He later claimed that language emerged as part of general symbolic capacity and said that while only humans had true language, “its roots probably lie in the power of the higher apes to solve specific problems by abstracting general forms or schemata from the details of given situations” (Radick 2007). This is a view of language origins that views general concepts as more difficult than specific ones. Hypotheses about language evolving from cognitive capacities tend to put mental grammar first, where problem-solving by tracking relations between concepts and organizing concepts systematically is the precursor to the combinatorial syntax that makes human language so productive.

In contrast to the idea that generalizations are at the root of language evolution, raven researcher Bernd Heinrich implicitly used the ability to be specific as a criterion for language. He states that raven vocalizations are “not used as language” because the specific meaning of calls

depends on context (Henrich 1999, 192); although his confidence in their level of specificity or vagueness is surprising, since he said in the same book that not much was known about raven calls. Specificity in prairie dog alarm calls was not detected without statistical analyses including various acoustic parameters in different contexts, so it is risky to assume a lack of specificity in an understudied repertoire. Heinrich may have been influenced by W. John Smith (1977), who claimed that all nonhuman animals have a limited number of general messages and that response specificity in is all supplied by context. Smith was unaware of many specific animal signals. Vagueness and specificity exist on a continuum; no communication system can be classified as totally specific or vague, as any signal may require more or less context to be understood.

Since Hockett, language has usually been defined in terms of some set of adaptive features. Many people refer to some of the more useful features from Hockett's list without mentioning Hockett or acknowledging that they are defining language as a set of design features. In *The Social Conquest of Earth*, E. O. Wilson described language as something that "uses arbitrary symbols and words to convey meaning and generate a potentially infinite number of messages", so his implicit criteria for language appear to be arbitrariness and productivity (Wilson 2012, 228). He also mentions "detached representation" (displacement, or the ability to refer to things distant from the signaler in time and/or space) and presents it as a feature unique to human language—no less than two pages after talking about bee dances, which are used to refer to food that is not present in the immediate vicinity. He later claims that no other communication system is able to refer to things that are not only displaced in time and/or space but that do not exist at all, but some forms of deception may be evidence against this. When great

tits use false alarm calls to clear sparrows away from a desired food source (Slobodchikoff 2012, 68) they must refer to a nonexistent predator. While many alarm calls may refer to a behavioral response instead of a predator type, the alarm calls of great tits are predator-specific even when their response to different predators is the same (Suzuki 2013). We do not know if the senders of false alarm calls consciously intend to create a mental representation of a nonexistent predator in the minds of the receivers, but the calls are clearly intended to make the receivers behave as if the predator in question had been sighted; they at least functionally refer to something that does not exist. The juvenile baboon in Byrne and Whiten's 1985 study who screamed to make his mother chase an adult from a desired foraging spot was also referring to a nonexistent event: a fictional attack by the adult on the juvenile.

One language feature on which Wilson focused is the ability to be indirect for diplomacy in large social groups. This is not a feature most researchers mention when defining language or discussing communication, but it is related to the use of small gestures to avoid outright conflict in social situations. An example of this is when a wolf snarls to drive other individuals away without having to fight. Gordon Haber observed adult wolves in Denali using gestures like this to drive energetic pups away from where the adults were trying to nap. Subtle gestures and diplomacy are not unique to language, but may have been important if language evolved primarily as "gossip" to maintain social alliances and exchange social information, particularly about who is trustworthy and who is dishonest. Cooperation is enforced more effectively when an individual's reputation within a social group can be communicated. In the absence of language, reputation builds on multiple individuals observing one's behavior, but with linguistic gossip only one individual is needed to witness an act of cheating to spread the information to

the rest of the group. In evolutionary game theory, free riders will quickly outcompete cooperators unless group members can communicate about others, allowing a groupwide tit-for-tat strategy; in modern humans, over 60% of speech consists of social topics (Dunbar 2004).

Con Slobodchikoff (2012), in a book directed at general audiences, never chose a single definition of language. He began with the idea that language is any purposeful communication or any signal that communicates the signaler's intentions, but he failed to resist the pull of Hockett. Throughout the book, Slobodchikoff recruits Hockett's design features to prop up various communication systems. The implicit language definition one can piece together from Slobodchikoff is that any purposeful communication system counts as language, but having some of Hockett's design features (including arbitrariness, syntax or grammar, displacement, and productivity) gives a communication system 'extra language points'.

For linguists like Noam Chomsky and Steven Pinker, the definition of language is grammar, primarily structural and genetic. It is not human-centric on purpose, but humans are the only known primates with some of the features important for this definition. One of Chomsky's central points about innate or genetic grammar is the fact that language-learning occurs too quickly and too accurately to be due to normal learning mechanisms. We also know of genes that deal with grammatical structure showing that genetically speaking, grammatical language is its own trait or collection of traits and not simply the combination of vocal communication and general intelligence. Nick Chater thought that grammar could not be genetically encoded because it changes too fast for evolution (Wilson 2012, 235), but this is

probably a matter of conflating specific grammars in individual languages (which change via cultural evolution, not genetic evolution) with the general grammar-acquisition ability.

Case studies involving pidgins and creoles demonstrate that humans have something unique among primates when it comes to grammar. A pidgin is vocabulary without grammar, often created by communities of adults who know different languages and combine the vocabularies into one set. The next generation in such a community will spontaneously form a creole, which is structured like a true language and has grammar that was absent in the initial exposure. This grammar is not learned from the environment but formed in ontogeny. The same thing happens to deaf babies learning sign language from hearing adults who didn't learn to sign until after they were too old for the spontaneous language-learning process. These adults tend to sign in pidgin, but their offspring generate grammar without being exposed to it (Bickerton cited in Pinker 1994). There must be a genetic explanation for the ontogeny we see in grammar to explain why human babies learn grammar when exposed to a pidgin, but chimps exposed to a human language or human-made artificial language always end up with a grammarless pidgin. Mutations in certain genes can disrupt grammar and language learning without having an effect on intelligence or other types of learning (Pinker 1994).

The genetic features that govern grammar and syntax in humans and which Pinker would equate to "language" are important because of their functions and because of what they allow in terms of learning, productivity, and semanticity even if one prefers a broader definition of language. However, this does not mean one should take these linguists' perspective and focus on humans and other primates at the expense of equally interesting convergences in other lineages. Marler's bird studies revealed parallels between birdsong and human speech related to ontogeny,

learning, and syntax. In both birds and humans, young learn from adults, learning results in dialects, there is a critical period for learning[18], learning depends on adult models and self-feedback, there are developmental stages (including a subsong or babbling phase in which the young individual repeats phonemes or units without syntax), and vocal communication is left-hemisphere dominant, apparently due to convergent evolution (Marler 1970).

Today, definitions of language continue to be muddled. Most definitions of language include both senses of the word "intentional"—the communication must be purposeful and it must be about something, meaning it must have semantic or representational content (Allen & Bekoff 1997)—as well as open-endedness or productivity which is usually achieved through discrete combinatorial syntax. Slobodchikoff tried to say that any purposeful communication is language, regardless of repertoire size, and even presence or absence of semantic content, but he also noted that open-endedness and flexibility are important qualities to consider. Pinker focused on the differences between human language and other species in order to define language in terms of what aspects make human communication so productive, including ontogeny comparisons and quantitative differences between language-learning and regular learning. Hauser pointed out that the syntactical structure of human language can't be compared to that of

[18] Marler's discovery of sensitive periods and the instinct to learn influenced developmental linguists in the late 80's-early 90's (Hauser 1996, 57).

most other species because we don't yet have the necessary information about semantic potential without knowing the relevant units of analysis.

One issue, apparent in the work of anthropologist Jane Lancaster, is a preoccupation with homologous structures. Lancaster said that a communication system is not a language (or "a step toward language") unless it shares a common ancestral trait with human language or is evolving to use the same mechanisms as human language (Radick 2007). In *The Language Instinct*, Pinker seemed totally uninterested in analogous traits and only cared about homology in language, which is as bizarre as someone who studies flight only caring about insect wings and having no interest in vertebrate wings even though they show that some vertebrates are under selection pressures that favor flight and that they developed an ability similar to insect flight but with vertebrate limbs and physiology. Analogous linguistic features should be at least as interesting to researchers as homologous ones. If some non-primate or non-mammal lineage has "true" linguistic capabilities by any definition, why would it matter if it didn't evolve from the third convolution in the Sylvian fissure in the left hemisphere?

When Von Frisch used the phrase "bee language", Hauser (1996) says he meant it as an analogy based on the communicative function, not as a claim for homology, but this is not to say that homology is required for a flexible, productive, open-ended, symbolic communication system to be considered language. Most laymen would call any form of symbolic communication a language. Slobodchikoff would include any purposeful communication system, but give extra "points" to systems with some of Hockett's design features. Pinker (and Chomsky) would only include systems with a genetic component which shares ancestral origins with that of humans and allows individuals to form a grammar more quickly than they could using regular learning. It

may be that if we define “true language” by Pinker’s standards, only humans will be found to possess it, but only using humans to define a character is likely to lead to a mistake like that of a moose biologist who claims that elk do not have antlers because true antlers are palmate. Only through comparison of multiple taxa and a willingness to concede that not every characteristic present in one species’ communication is necessarily diagnostic of language can we avoid this kind of mistake. Convergent evolution in multiple lineages facing similar demands on their communication abilities is not a distraction from homologies, but an important area of study that could lead to a more objective definition of language.

Study of semantic communication, placed in some relationship to the language debate and honest interest in the origins of humans’ complex syntactical language, tends to drift back toward what Tinbergen criticized behaviorists for in the 30’s and 40’s—“looking for the prehuman in the animals” rather than studying the animals for their own sake. But as much as we should avoid using other species as models for our own, humans should not be left out of the field either. Human language also deserves to be studied for its own sake, and it serves as a useful foil in studying other communication systems. When semantic researchers use different methods of analysis for humans and other species, is it because they know how the signals are structured differently, or is it because they only know the basic syntactical units for human language and are using methods that assume syntax is not present in other species? Whatever turns out to be unique in human language, we should ask how it evolved, what is adaptive about it, and what was unique about early human environments that favored these traits. But before

declaring that a language feature is unique, we must apply consistent methods across taxa, ask about analogies as well as homologies, and examine environments that select for those features.

Researchers should be wary of ignoring traits that may be unique to other species and of assuming things about the usefulness of a communication system that does not share a certain feature with humans. It is also important to study species under similar selection pressures to humans (or other species whose communication is well understood) that have different combinations of communication features and ask why they are different. What makes a species need combinatorial syntax or productivity? Would one species benefit from a linguistic trait that another species has, but cannot evolve it even under the same selective conditions because they lack some preadaptation? Communication research should focus on the kinds of evolutionary and ethological questions that emerge when similarity to humans is not held up as the only benchmark for deciding to take interest in another species' communication.

There is another reason why humans gravitate towards defining communication systems as language that has to do with how humans behave when they believe that a species has what they consider 'true language'. When Garner set out to attempt playback studies of wild primates, he fully intended to discover a language and learn how to translate it. He addressed the humans who were possessive of language as a unique trait:

> A knowledge of their language cannot injure man, and may conduce to the good of others, because it would lessen man's selfishness, widen his mercy, and restrain his cruelty. It would not place man more remote from his divinity, nor change the state of facts which now exist. Their speech is the only gateway to their minds, and through it we must pass if we would learn their secret thoughts and measure true distance from mind to mind (Garner quoted in Radick 2007).

Garner thought that if humans could learn what animals were thinking by knowing their languages, they would behave better in their dealings with other species. While this prediction ignores nonverbal communication or "body language", non-linguistic vocalizations that express emotions, and the fact that humans are selfish and cruel to other humans whose languages they already know, Con Slobodchikoff says that humans react positively to the mere existence of language or language-like communication. When he tells audiences about the semantic abilities of prairie dogs, they gain respect for a species they previously thought of as a pest. Slobodchikoff discusses the ecological importance of prairie dogs as well as their language, but it is consistently the language rather than the ecology that makes humans stop wanting to kill them off. He favors a broad definition of language because calling an animal's communication system a "language" causes humans to gain respect for the animals because they are already used to respecting the idea of language.

The problem with this approach is that it depends on humans all agreeing on a definition for "language", which is not likely to happen in the near future. Slobodchikoff is interested in bridging the apparent gap between humans and other animals, and he decided to go after language because it is one of the last things holding that gap; but whatever you observe in another species—semantics, grammar, specificity, or general concepts—those who are invested in human uniqueness will simply redefine language such that it only includes humans and ignore any broader definitions.

Humans have put language on a pedestal and people like Slobodchikoff want to use that pedestal to stop humans from behaving badly toward other species. But the pedestal holding "language" actually sits on another pedestal which holds "intelligence". Evans (1891) placed

value on intelligence the way Slobodchikoff places value on language: “It is evident that the barrier between human and animal intelligence, once deemed impassable, is becoming more and more imperceptible, and with the rapid progress of zoopsychological research will soon disappear altogether”. Humans often base their respect for other species and their willingness to protect their welfare on perceived intelligence, which they also associate with emotions, but according to Marc Bekoff (2007) there is no evidence that intelligence or relative brain size affects how emotional a species is. It also does not affect their capacity for suffering, which should be the basis of ethical decisions like those Slobodchikoff wants to promote. Pinker, who does restrict language to humans, would rather knock down the pedestal entirely—so what if only humans have language? Every species has traits uniquely adapted to their environments. One interesting trait in one species does not make other species any less interesting or valuable.

For their own sake, humans should not base their level of respect for other species on the presence or absence of humanlike language. There is no virtue in valuing only what is most like oneself. There may be a much stronger argument for abandoning “language” altogether, especially if almost every definition relies so heavily on humans that it fails to make sense in a comparative framework. It is difficult to come up with a definition of language that isn’t human-centric by definition but also avoids being so vague that it includes all purposeful animal communication. If “language” is to be used as a category, it must be defined objectively based on comparative research across taxa; but if the question of whether or not various communication systems count as languages is derailing or distracting from actual evolutionary, ethological, and cognitive questions, there is no reason to keep the word “language”. One can borrow methods from linguistics and study communication systems and their features, structures, evolutionary

history, adaptiveness, genetic components, functions, ontogeny, and cognitive implications without calling anything ‘a language’ or ‘not a language’.

In reality, “language” may not be anything in particular. It is not useful to argue about language instead of looking at which combinations of traits exist in different communication systems and how they work together. Lists of features that must exist in a communication system to make it a language like Hockett’s and those that followed may be just as irrelevant as precisely documenting the exact shape, size, and color of an elephant’s foot and calling it a definition of feet. The particular combination of traits that most human communication systems have may be unique to the species, but other species also have unique combinations of communicative traits. Researchers should study communication in as many species as possible to determine what they can do and why their gestalt of communicative abilities is adaptive for their particular communication needs.

If language cannot be stripped of its anthropocentric definitions, and if it has a detrimental influence on the way humans act toward other species, maybe it is unnecessary. We have other ways to talk about communication and its adaptive features that apply to the world as it is instead of a world where the implicit goal of evolution is to become more like humans. Language is not one trait but as a name for a kind of communication system resulting from the intersection of several ‘powers’ such as syntax, combinatorial thinking, and specific semantic meanings in a complex social environment. As we move forward in the study of communication with or without “language”, we should approach it from a comparative, ethological perspective and explore the diversity and flexibility of communicative systems and behaviors throughout the animal kingdom.

CHAPTER THREE

HUMANS STUDYING HOWLS

> *Wolf howls, for example, chilled the spines of Euro-American colonists from Maine to Montana. Colonists proclaimed the yowls haunting, devilish, foreboding. Engrossed in the projects of livestock raising and territorial conquest, Euro-American settlers were poor listeners. In post-World War II United States and Canada, better listeners asked new questions about wolf howls. Instead of trying to determine what the howls meant to them, wildlife biologists wondered what the songs meant to wolves.*
>
> –Jon Coleman, 2004

This chapter will review the literature on wolf howling in North America and Europe. Trends in questions, study locations, methods, and the recruitment of technology and other elements from different fields will be identified in each decade from the 1960's to the 2010's. The trajectory of wolf howl research points toward predictions and recommendations for future research on how and what wolves communicate in their howls.

One may expect that the kinds of questions asked about wolf howls would follow the ecological status and cultural perceptions of wolves over time and space, and that earlier wolf howl papers in North America would have focused on ecological questions regarding what howls can tell us about predation, pack movements, and the status of threatened or recovering populations while questions about what howls mean to wolves and what they indicate about individual wolves and their relationships would be found in later publications. But in fact, questions about potential information in howls and attempts to discern meaning using howl variation and correlated behaviors or stimulus conditions are as old as wolf howl research.

These questions (semantic, syntactic, and approaching linguistic) have failed to progress to the point where one could "translate" a howl from a recording because of several factors. Tradeoffs between studies in the wild (accurate context and full range of normal behavior) and in captivity (ease of access and ability to match howls to howlers), the lack of consistent methods for describing continuously varying vocalizations, and the fact that most of the research interest is in other aspects of wolf behavior limit the scope and possible results of wolf howl studies. Wolf howl studies in the wild tend to focus on questions about the presence or absence of howls instead of howl structure and characteristics, and when aspects of howl structure are included they're used to answer questions about who is howling (how many adults, how many pups, etc.) rather than what the howl means semantically. Most studies of howl characteristics, type, and structure are about individual ID, and while these consistently find that howls carry individual ID information, each paper concludes with a different set of variables that were found to be important in identifying individuals. The description and analysis of continuous vocalizations continues to face challenges that do not exist for calls made of discrete units. While questions about howl meanings have been simmering since the beginning of wolf research, they are often overshadowed by non-howl questions about behavior or by non-semantic questions about howls.

Review of Wolf Howl Papers Over Time

Papers specifically about wolf howls first emerged in the 1960's. The ecological studies of wolves that began to appear in the 1930's-40's often included brief observations of howling behavior, but there was not enough information to warrant dedicated papers on howls. Howling responses were used as a tool for humans to locate wolf packs for ecological and territorial studies or to track pack movements (Pimlott 1960; Joslin 1967).

Aside from neutral descriptions and papers on how humans can use wolf howls, the first paper that investigated how wolves use howling to communicate was published in *American Zoologist* in 1967 by John B. Theberge and J. Bruce Falls following Theberge's M.A. thesis of the previous year. They asked five questions about the properties of wolf howls, variation in howls and potential correlation with context, ability of wolves to detect variation, the circumstances around "spontaneous" howls (those that are not responses to auditory stimuli), and the ecological role of howls. They found differences in howls between individuals, auditory discrimination sufficient for wolves to detect those differences, and increased howling by isolated wolves, but nothing about possible social or behavioral-selection messages. There was evidence that howls contained information about howler identity, howler location, and possibly separation from the group, but nothing conclusive was found about semantic messages.

Theberge and Falls asked directly about the communication potential of howls—"Does variation in wolf howls relate to behavior or any circumstances surrounding howling and thus represent units of potential information?"—but were unable to answer satisfactorily due to methodological constraints. They analyzed howls with recordings and spectrographs but also by ear with a pitch pipe, describing frequencies in terms of notes like C# high instead of kHz. They divided howls into three arbitrary sections and identified types of beginnings, middles, and ends based on arbitrary quantitative definitions of things like "abrupt", "gradual", and "sudden" and non-quantitative categories that are irrelevant to wolf ecology like whether a human can discern the last note by ear. The behavioral contexts they looked at were lying, walking, and pacing; none of which are socially relevant on their own and all of which could be associated with a wide variety of mental states or intentions. They found some associations between types of "middle"

and pacing, but other relationships were specific to each individual (Theberge & Falls 1967). While the authors guessed that familiarity with an individual would enable wolves to interpret their howl variations, it is more likely that the small sample size, arbitrary ways of classifying howl segments, and socially irrelevant choices of behavior caused the appearance of each wolf having an individual 'code'. For a behavior to be worth communicating about, it needs to have a social or ecological function, and the communication must benefit the fitness of at least the sender. There are probably mental and emotional states associated with responding to a howl stimulus and spontaneously howling when isolated and trying to locate one's group members, dependent on the personality and temperament of the individuals in question, and individuals may have movement habits associated with these emotional states. With a combination of captive and wild observations, one might be able to discover that an activity like pacing in captivity would normally manifest as an attempt to do a socially relevant action that is worth communicating about such as traveling toward separated packmates.

Theberge and Falls cite Gunter Tembrock (1963), who briefly speculated on the possibility of different howls with different messages. Tembrock mentioned that howling "seems to have certain variants, possibly with different functions" with no citation and no further elaboration. He speculates about the function of chorus howling or "singing in unison", but he doesn't mention social cohesion as one would expect. Instead he talks about chorus howls indicating that wolves are occupying a territory, scaring off other groups, and calling back lost members before or after hunting. The speculations here are preoccupied with hunting and territorial defense.

Theberge and Falls asked some important questions that predicted several directions wolf howl research would take in the coming decades, but their ability to answer them was extremely limited. They were only able to collect howls from three wolves. These wolves were born in captivity and had been living in separate pens at a research station since the age of 1 month (a backstory which implies they are brothers from the same litter, but the paper does not confirm). All three were male. One cannot expect to make ecologically relevant observations of social and communicative behavior in a setting with no packs (not even an artificial one), no pups, no females, no territories, and no hunting; or to learn anything about the variation in howls from three individuals who were probably closely related. At that time, access to high-quality captive populations was rare, and the opportunity to study wolf behavior in the wild was even rarer.

Two years later, Theberge began publishing on wild wolves in Algonquin Provincial Park, using recordings of pup howls to elicit responses and locate wolves in the forested park during late summer, when pups were at rendezvous sites and a few adults generally stayed nearby but out of sight. This study included descriptions of a "greeting ceremony" which took place when pack members returned to the rendezvous site and "frolicked together in a tight group" with "vigorous flicking of tails" (Theberge 1969); Theberge did not mention howling in the greeting ceremonies, but they sound like rallies as described in the wolf ethogram from Goodmann et al at Indiana's Wolf Park (2002)—"pressing together with tail wagging, greeting", and friendly displays including whining and soft muzzle-grabbing—which are often seen before and during chorus howling (Harrington 1989). Along with responses to human-generated howls, whether emulated by humans themselves or playback of recorded wolves howling, the observations in Algonquin Park included "spontaneous" howling on nights when a pack member

was absent, showing that separation of pack members elicits howling in the wild and that “at least one type of howling is a manifestation of an emotion triggered by separation, and has an obvious value in pack cohesion” (Theberge 1969).

Researchers studying the contexts of howls in the 1960’s-70’s focused on wolves in isolation. In his 1976 paper describing canid sounds and sorting them into groups based on phonetic characteristics, Tembrock speculated that “chorus crying could also serve as an advertisement of territory for groups and thus influence the density dispersion of populations”, but territorial howling was less of a focus than howling in isolation. Young & Goldman called this a “loneliness cry” and others have called it a “separation cry”, but nobody mentions acoustical differences between these solo howls and chorusing. According to Tembrock, older papers described canid vocalizations based on their presumed meanings or functions, using descriptions of emotional states. Tembrock divided vocalizations into those triggered by external events, which are derived from an explosive expiration and include yelps and “forced-out breathing sounds”, and those controlled by the animal’s internal state. He classed howling as a controlled vocalization with multiple functions depending on whether the howler is alone or in a group, including the function as a long-distance contact call after Theberge & Falls.

Another 1976 paper, an investigation of vocalization types across various wild canids and domestic dogs in different social contexts by Cohen & Fox, classified call types by visual inspection of spectrograms and discussed their ontogeny and structure. They noted continuous gradations between sound types and the fact that vocalizations can be mixed, either by using an intermediate call type or by using multiple call types in succession, indicating mixed motivational states. Here, vocalizations are paired with their social contexts and interpreted in

terms of arousal levels and motivation or intentions. Cohen and Fox describe canid vocalizations as an “emotional language” rather than a semantic one, analogous to the paralanguage in human speech consisting of nonlinguistic tones, postures, and expressions that convey information on the speaker’s emotional state.

In the 1970’s and 80’s, the wolf howl research in the wild was dominated by North America, and a majority of papers came from the Superior National Forest in Minnesota. Fred Harrington, originally a psychology professor, joined Dave Mech on the SNF team to study wolf ethology, ecology, and communication. Two of their papers provided experimental support for the previously observed role of howling in territory maintenance. In 1978, they studied responses given by wild wolves in different conditions to simulated howling by humans. Wolves in the SNF were known to respond to human howls as if they were strange conspecifics (Joslin 1967), so this was effectively a study on how several packs in the SNF responded to alien howling within their territories. Several of the variables in this experiment were only known because the population was the subject of a larger ongoing study involving radio collars and planes with which to locate wolves, detect movement toward or away from a howling stimulus, identify rendezvous sites, and detect kills.

Harrington and Mech found correlations between howling response rate and variables known to correlate with extra-pack agonism, including pack size, social role, pack membership, and breeding season. A territorial message was also implied by the way movement was related to vocal response—wolves who howled in response to the humans remained where they were 90% of the time, while wolves who did not reply only remained 67% of the time. Response rate was

also higher when the wolves were in the presence of an important resource, whether it was a reproductive resource or a food resource, and declined proportionally to the wolves' need to defend the resource (as a litter of pups grew up or as a carcass was consumed). Harrington and Mech framed these results in terms of an expected strategy based on the costs and benefits of howling. Howling lets a wolf avoid accidental encounters, but staying silent lets them avoid deliberate encounters or attacks. Retreating without howling would avoid both, but this could mean giving up an important resource. As expected, howling responses in the study were not associated with a pack's entire territory, but specific immovable resources like carcasses and young pups at rendezvous sites.

The authors noted that because they howled from inside the resident pack's territory, they were seeing how the pack responded to an apparent intruder. Because intruders are more likely to attack a resident pack than other wolves howling from their own territories would be, the resident pack's response rate may change based on the amount of perceived danger from a stranger howling from inside or outside the residents' territory, but "the limits of human hearing and the large pack ranges prevented us from testing the above speculation" (Harrington & Mech 1978).

Because Mech was involved in multiple studies of wolves in the SNF, he and Harrington were able to include additional data about territorial messages in the howl response paper. Peters and Mech (1975) were studying the same packs at the same time as the response rate experiments of Harrington and Mech, so they were able to pool the data and discover that howl response rates and raised-leg urination rates were similar within each pack and varied between packs in the same way. They considered scent marking and territorial howling to be

complementary signals with the same messages, one long-term and site-specific and the other immediate and long-range.

In a 1983 paper, Harrington and Mech focused on the spacing and territorial mechanisms of wolf packs to determine how they achieved exclusive territories. They used the same method to ask whether howling responses, like scent marking, were concentrated near borders and buffer zones. Some arbitrary decisions about how to measure variables such as response rate and location with respect to territory centers were inevitable. Outside of homesites, there was no effect of location on vocal response; while howling response rate depends on the presence of resources that are temporarily associated with certain locations, it is independent of the location within a pack territory. Harrington and Mech did not obtain any information about the spatial distribution of non-elicited howls, as they did not have the equipment, hearing range, or time to assess whether spontaneous howling was more or less frequent in buffer zones. At this point in the timeline, non-territorial howls in the wild have yet to be studied because only territorial howling can be easily elicited by humans.

Harrington was responsible for the first paper directly comparing the structures of howls associated with different behavioral contexts. He asked about structural differences in howls associated with different behavioral responses to playbacks of strange wolves in a pack's territory, looking for structural changes that would indicate "changes in underlying motivation" (Harrington 1987). Possible responses to a stranger howl were ranked by their level of "aggressiveness", meaning "probability that the responding animals might eventually encounter the strange wolves and an attack with injuries or death may result". Responders can retreat,

remain, or approach; and they can do each of those either silently or with a vocal reply. Replying was rated as more aggressive than staying silent because it reveals the responder's location. In Harrington's study approaches always followed an initial "remain and reply", as wolves never approached silently or with reply unless they'd already replied from their original location. Other humans who have elicited responses from wild wolves by howling have observed resident wolves approach the humans silently without first remaining and replying (Theberge & Theberge 1998). Harrington was looking for differences in frequency and noisiness because of Morton's motivation-structural rules which state that many birds and mammals in aggressive behavioral contexts use vocalizations that make them sound larger. Close-approach howls did have lower frequencies than other samples of howls from the same packs. While this study did not collect enough data to statistically control for size, Harrington had enough observations to conclude that the difference was not simply due to larger wolves being more likely to approach a strange howler. Collected observations from individual wolves revealed that the close-approach howls of individuals were lower than their other howls, including howls in the same interaction before they approached, and that at least some wolves use lower howls at the point of closest approach than they do while approaching. Sometimes "coarse" qualities (harmonically unrelated sidebands) were present toward the end of the close-approach howls. These noisy ends, as well as barking which was sometimes used in exchanges between approaching residents and (playback) strangers, would make the approacher's howls particularly easy to locate.

Until the end of the 1980's, measurements in howl papers were fairly basic. Harrington's next howl paper in 1989 began to use more complicated variables to describe howl structure,

including the coefficient of frequency modulation and coefficient of frequency variation, measurements of frequency changes calculated after sampling the fundamental frequency of a howl every 0.2 seconds. Harrington used the same method of eliciting howls to investigate the ability of chorus howling to convey information about pack size and the potential for the chorus structure to obfuscate or exaggerate the true number of wolves. The fact that the population was part of the same ongoing study in the SNF meant that pack size and composition were known, and pack composition during howling sessions could often be inferred based on observations and radiotelemetry revealing which wolves were away from the pack at a given time (although the locations of uncollared wolves was unknown without incidental observations).

Humans have attempted to count wolves by counting entries into a chorus, but there is no way of knowing from sound alone whether the same individuals are re-entering. Harrington notes historical and contemporary instances of humans guessing that a chorus was made of at least four adults with several pups only to discover that it was actually a single adult pair.

Harrington quantitatively verified that howls later in a chorus are more variable and increase in measures of frequency changes, but only when the pack members were together while howling. CoFM and CoFV did not increase during chorus howls where pack members were scattered. In this case, specific measures of frequency modulation and variation quantify a phenomenon that is regularly observed by visual inspection of a spectrogram or by the naked ear in the field. Increased frequency modulation over the course of a chorus howl introduces more confusion with echoes and reverberation of different frequencies, and receivers unable to match echoes with their sources perceive them as multiple voices. Chorus howls could have evolved to disguise pack size, but not necessarily to exaggerate it except in the cases of very small packs.

This paper was analytically limited by the accessibility of each pack and the difficulty of extracting howls out of a complicated chorus with reverberations. This remains a problem for wolf research, and many papers involving chorus howls only analyze the initial howl because it is simple in structure and easy to discern.

In the 1990's, after the discovery of individual ID information in the calls of several other mammals, interest turned to individual ID in wolf howls. The SNF team was able to answer important questions in the wild because they had access to data, information, and collared wolves from the ongoing project. When it came to questions about individual identity information available in howls, however, researchers had to make a tradeoff between the full evolutionary context of a wild wolf pack and the experimental abilities allowed by captivity—specifically the ability to elicit howls while controlling contextual variables and to know which recorded howls belong to which individuals.

The first paper providing statistical confirmation that individual wolves have identifiable howls came in 1990. Harrington worked on this project with a biologist and another psychologist. They collected a sample of howls from each of seven captive wolves at facilities in Nova Scotia and Minnesota. All howls were elicited by and recorded in isolation from the other wolves, ensuring similarity in howl context and making it easier to obtain high-quality recordings (Tooze, Harrington, & Fentress 1990). Quality may have been limited by the fact that they had to record howls onto cassettes and then copy them to tapes for spectrograph analysis. This is the most statistically explorative howl paper so far, looking at 14 total variables in 3 categories: modifier variables regarding the number of harmonics and duration of sidebands,

pitch variables about the fundamental frequency, and shape variables attempting to describe the fundamental frequency contour or how it changes over time during the howl. They used principal component analysis (PCA) and discriminant function analysis (DFA) to identify which characteristics were most important for discrimination between individuals, finding that the most important principal component for individual discrimination correlated with fundamental frequency variables. The discriminant functions were able to reliably assign howls in a holdout sample into the correct groups at 86.5% success.

This paper was written after vocal signatures involving frequency variables had already been found in many other mammal species, so neither the question nor methods were new. Papers about individuality in the calls of mammals, including other canids (Durbin 1998), were published throughout the 80's and 90's. The relevant socioecological question is something like 'do wolves recognize individuals by their howls?' and Tooze et al made the first step in answering it by showing that howls from different individuals are actually different.

In the 2000's, more howl papers were published outside of North America. There were questions about how different populations and subspecies compared to the North American wolves in the literature, censusing methods, and increasingly technical howl descriptions. Wolf howl studies started to come out of Mexico, Italy, Spain, and Poland, both in captivity and in the wild. Several European papers from the 2000's framed their research as something already known about North American wolves that had yet to be fully described in other populations and subspecies and compared with North American wolves, and discussions almost always include a comparison to the wolves of the SNF (Gazzola et al 2002, Palacios et al 2007, Nowak et al 2007,

Passilongo et al 2010). Eurasian studies began to gravitate toward wild populations as the limits of captivity were recognized (Passilongo et al 2010).

The first study of howling in Mexican wolves (Servín 2000) showed that the frequency and duration of chorus howls both peaked in breeding season as it does in wolf populations in the US, Canada, and Europe; it also revealed a latitudinal pattern in chorus durations. Another study related to howling temporality came from a wild population in Italy characterized by small packs and territories, frequent contact with humans, and low-visibility mountain and forest habitats (Gazzola et al 2002). Monthly response rate peaked in late summer/early fall with a maximum around September-October; unlike spontaneous howls, the response rate for elicited howls did not respond to the breeding season. They were least likely to respond in May-July, verifying observations in captive wolves indicating that adults are reluctant to howl until the pups are 6-9 weeks old, at which point the pups begin to howl and initiate some choral responses themselves. Winter response rates were low as packs abandoned their homesites.

The howls of Iberian wolves, another neglected subspecies, were described in 2007 by Vicente Palacios, Enrique Font, and Rafael Márquez. These researchers described the acoustic structure of the howls from captive wolves held in several locations within their natural range and assessed their ability to communicate howler ID. Description of acoustic structure included fundamental frequency variables, inflection points and discontinuities, location of peak amplitude, and coefficients to describe frequency modulation and variation. Based on discontinuities and modulations, howls were assigned to four categories which humans can diagnose by looking at a spectrogram: flat, breaking, continuous wavy, and breaking wavy; only two of which (flat and breaking) had been identified by previous authors. Using a similar method

to Tooze at al (1990), they identified the most important variables for discriminating howler ID as several fundamental frequency variables and the number of harmonics.

Nowak et al (2007) studied spontaneous howls in Poland by radiotracking collared wolves. This study was a response to the lack of knowledge on temporal and spatial patterns of spontaneous howling year-round, as previous year-round studies used elicited howling and previous studies on spontaneous howling focused on spring and pup-rearing season. Nowak et al discovered differences between the patterns of spontaneous and elicited howling such as infrequent but regular spontaneous howling during early denning season, when wolves do not respond to simulated or playback howls, high rates of intrapack howling during pup-rearing season, and low rates of spontaneous howling in winter when territorial response rates are higher. They also found that the previously observed peak in howling during breeding season was primarily a function of response rate and not spontaneous howling. They found that both spontaneous and elicited howls peaked in August, wolves only responded to human howls in June-September, spontaneous howls peaked just after sunset, and wolves howled from the centers of territories. Without radiocollars, studies of spontaneous howling rates were restricted to spring and summer when packs stay at dens and homesites; radiotracking allowed Nowak et al to map howling rates year-round and determine where wolves were howling. For most of the spontaneous howls, observers were able to identify the social contexts[19], but they did not attempt

[19] 43% communication between temporarily separated packmates, 18% howls by the whole pack after reunion, 22% setting off on a hunt, 5% at a fresh kill, and 2% howling between neighboring packs (Nowak et al 2007).

to use these categories as classification variables to see if howl structure responded to the context as they were primarily concerned with howling rates and temporality, not acoustic structure.

More interest in howl structure emerged in the next decade. Many papers were on identity information: individual, group, population, and species/subspecies. Concern with population monitoring continued, and the acoustic energy distribution of chorus howls (most emitted in response to human howls) were used to confirm the presence of pups in a pack, as choruses with pups had more energy in the higher frequencies (Palacios et al 2016). A few papers continued to assess responses to howls and other factors that influence howling behavior. To classify howls into groups, earlier papers used discriminant function analysis with many variables describing howl features, but in the 2010's more papers began to use a principal component analysis first to obtain a small number of variables containing correlated howl features and then using the principal components as variables in the DFAs (Passilongo et al 2010, Root-Gutteridge et al 2014a and 2014b). Social factors and contexts of howling were also questions in 2010's captive studies (Mazzini et al 2013, Watson et al 2018).

Earlier papers on individual ID information in howls focused on frequency variables, but amplitude variables also contribute to individual howl differences. Because other mammal vocalizations were found to encode individual ID information in amplitude variables, Holly Root-Gutteridge included amplitude variables in an individual ID analysis and found that changes in amplitude improved individual ID of howls in captivity (Root-Gutteridge et al 2014a). This method was then applied to wild wolves recorded from unknown distances in variable conditions (Root-Gutteridge et al 2014b); this was the first attempt at identifying

individual wolves from their howls in the wild. Normalized amplitude variables of the first 4 harmonics were used to ID individual howls in captivity and in the wild, but harmonics 2-4 could not be measured accurately in chorus howls and low-quality recordings.

Root-Gutteridge et al also contributed to the problem of extracting howls from noise in a recording. They compared a standard method using Praat with an alternate method using a Matlab script to extract howls from background noise by fitting the sound spectrum to four Lorentzian peaks forced to be exact multiples of each other, which excludes background noise and other features which were not multiples of the fundamental.

Continuing the process of inquiry into individual ID begun by Tooze et al (1990), Palacios et al (2015) used a habituation-dishabituation paradigm[20] to assess the ability of captive wolves to recognize differences between howls from different wolves and between normal and modified playback stimuli. Wolves habituated to new howls from the same wolf as the original playback stimulus, but showed a dishabituated response to howls from a different wolf. They also responded to the habituated howl played backward (a stimulus with the same frequency and frequency modulation variables as the habituated howl but in an unfamiliar sequence) and to modified howls in which the frequency varies outside of the normal range for an individual. These methods had been used in other species but were applied to wolves for the first time here.

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[20] Subjects are habituated to stimulus A by repeated exposure (leading to a decreased response) and then presented with stimulus B. Showing a dishabituated response to B and a habituated response to a subsequent instance of A means the subject can tell the difference between A and B. Howl stimuli were recorded from other captive wolves of the same subspecies who were unknown to the subjects and never heard before the experiment.

The question of group membership information in howls came up in 2012, when a paper compared howls of five Italian packs using frequency and shape variables and found significant differences in howling between different packs (Zaccaroni et al 2012). The howls were part of choral responses to playback stimuli. The question of group signatures is one example where it makes sense to elicit howls with a playback stimulus to control for context in the analysis. Two packs in close proximity with known intermigration were not distinguishable. The differences in packs in this study could have been due to the contributions of a few individuals, as it was impossible to know which non-overlapping howls belonged to the same individuals; the study also did not attempt to control for relatedness.

Another question that appears in the 2010's is that of global differences in wolf howls and the relationship of howl differences to species, subspecies, and genetic lineages. Arik Kershenbaum et al (2016) compared howl type histograms across canid species and subspecies and found species-specific patterns of howl type usage. Frequency modulation was described using an image-processing ridge tracker and by fitting harmonics to a Lorentzian function. Individual howls were compared using a dissimilarity matrix based on how much time distortion was required for each pair of howls to match the curves. Then a clustering algorithm was used to group howls into types based on similarity. Vocalizations were sorted into types with an automated clustering technique and histograms of type usage in different species and subspecies were compared rather than individual vocalizations from different repertoires. In the same paper, they applied this method to a question of management interest in North America by doing a separate analysis of coyotes, red wolves, and Eastern timber wolves. They found that red and

eastern timber wolves were similar, red wolves shared a most common howl type with coyotes although their type-use histograms differed, and one howl type found only in red wolves may be an intermediate type pointing to hybridization.

Another group compared howls from three basal mitochondrial lineages of gray wolf to each other and the Holarctic clade to test the hypothesis that howl structures correspond to phylogeny. Based on principal components correlating with frequency and shape variables, this analysis found that acoustic differences were largest in the Himalayan and North African clades which diverged before the radiation of the Holartic clade in the Northern hemisphere, corresponding to geographic and genetic distance (Hennelly et al 2017).

Questions about complexity in bioacoustics centered on birdsong in the 1980's but soon expanded to other species, despite a lack of consensus on which complexity measurements were biologically relevant. Researchers were interested in communicative complexity as a sign of cognitive development, as an indicator social complexity, and in relation to language evolution. Measures of complexity have also been used as just another phenotype that varies geographically, by population, and with individual health or quality. In 2017, Kershenbaum et al examined the acoustic complexity of wolf howls using various metrics and evaluated the relevance of the metrics to different kinds of hypotheses. For birds, repertoire size has been used as a simple measure of complexity, but this idea cannot be applied to continuous frequency modulated signals. Neither can traditional ideas of complexity bring the amount of entropy in a signal, as the highest-entropy signal is random noise and not biologically meaningful. Different measures must be used deliberately with the subjective qualities of the vocalizations in mind (for

example, autocorrelation measures the repetitiveness of frequency modulation in a signal, which can reveal redundancy, but it also makes random noise look complex; counting inflection points leads to a measure of complexity based on how many times a signal changes direction but does not capture all the variation in frequency within rising or falling sections of the signal). Drawing from previous studies of dolphin whistles, the authors also suggest using Parson's entropy to convert the continuous signal into a series of discrete characters using categorical bins for the magnitude of the slope of each time slice; then the Shannon entropy can be measured in terms of the probabilities of step categories just as it would be for a naturally discrete signal like a birdsong (Kershenbaum et al 2017). This paper encourages researchers to check objective measures with subjective assessments to verify that the measurements are evaluating complexity in a way that agrees with how an animal would interpret it.

The 2010's saw papers assessing field methods as well as analysis methods. In 2019, Kershenbaum et al published on a multilateration method for locating howling wolves using time differences from passive recording stations synchronized by GPS. This was framed as a way to use the vocalizations most common at night to locate wolves when visual sightings and radiotracking may not be possible and to monitor locations over long stretches of time, which is useful for behavioral research as well as population monitoring and management. While it was generally known that simulated howling could disrupt the normal activities of wild wolves (and hence playbacks and human howling were banned in national parks like Yellowstone), wolf-howling continued as a research or censusing method and as a tourist attraction in Algonquin Park, and the effects on wolf behavior were not quantitatively demonstrated until 2017. The movements of GPS-collared wolves in Quebec were tracked after simulated howling sessions,

revealing a slight tendency to group the pack together following howl stimuli and a difference in reactions to howl stimuli based on the howling station's distance from the pack's territory in this study vs. others where howling was conducted closer to rendezvous sites (Leblond et al 2017).

The first attempt to systematically describe non-howl vocalizations in the structure of choruses was also published around this time. Non-howl calls from choruses were grouped into six types based on a clustering analysis with silhouette information indicating a six-group model to be the best fit based on the fundamental frequency contour. The frequency variables and variables for noisiness and energy were condensed to three principal components which were used for a DFA to validate the cluster analysis classification of call types (Passilongo et al 2017). Call types identified this way corresponded to barks, whines, growls, whimpers, squeaks, and yelps. The authors claim that these call types may be useful for long-distance communication because of their presence in choruses, but it is more probable that at least some of the call types other than howls and barks are directed at packmates. The "short-distance" call types like whines and yelps and the "long-distance" howls may serve different functions in the chorus: group bonding and social cohesion functions that elicit emotional/affective synchrony and possibly function as vocal grooming vs. territorial advertisement directed at other packs.

More studies on the functions and uses of howling appeared in this decade as well. One asked whether emotional state or social factors contribute more as a releaser for howling (Mazzini et al 2013). Howls were elicited by the removal of an individual from a group of captive wolves in Austria. The elicited howls were analyzed in terms of the missing wolf's rank, the howler's relationship to the missing wolf, and the howler's HPA stress response (circulating

cortisol). Linear mixed effect models were used to determine how much each factor contributed to howling. Individuals howled more when they had more affiliative interactions with the absent wolf, showing that howls were primarily driven by the affiliative relationships of the individuals. Cortisol levels also did not improve the explanatory power of the model, meaning that removal of preferred individuals did not necessarily cause more howls by increasing stress. Because social dynamics in wolves are complicated and flexible, howling in this context was deemed "more likely to be modulated by cognition" than by physiology or emotional state. Mazzini et al looked at the number of howls, but no acoustic features or howl types.

At long last in 2018 we see the first captive study showing structural differences in howls produced in different contexts, which may correspond to differences in meaning or semantic content (Watson et al 2018). In three captive packs, howls elicited by the removal of a pack member were effectively discriminated from spontaneous howls based on duration, frequency, and energy variables. The authors used Praat for acoustic measurements, determined factors related to individual howler phenotypes and howling context with a DFA and PCA, and then fit a generalized linear mixed-effects model to see which principal components vary between howling contexts while controlling for individual. Because the 'elicited' howls in this study were from wolves attempting to locate a missing pack member, the howls may be different from those in a spontaneous chorus because of differences in emotional content rather than semantic content. The stressfulness of the situation may be magnified because the wolves are in captivity and cannot travel while howling in order to locate and rejoin with a separated pack member. While missing out on realistic wild contexts, this study was able to control for the effects of individual howler differences because each howler was known in captivity; but the small sample size

resulted in a failure to find differences between age classes (body size) and in being the only study that did not find fundamental frequency to be significant for individual ID. Regardless, this study was the first to do a quantitative analysis of howls in different contexts and may pave the way for studies of howl structure in more contexts, including in the wild, and playback studies examining responses to howls from different contexts to see what wolves recognize in the different howl structures and what kinds of semantic information (as opposed to individual ID characteristics and affective tones) howls are capable of transmitting to other wolves.

Ideally, the direction of semantic questions in wolf howls will use captive studies to the extent that they remain useful, but eventually this research will have to go into the wild where howl recordings must be combined with hours of behavioral observation to understand the full context and the nature of receiver responses. This necessity may drive some researchers away from accessible areas like Yellowstone and into places like Ellesmere Island where wolves are willing to display their full range of normal, relaxed social behavior even in the presence of humans and their equipment. While the endangered status of wolves in some decades drove funders toward purely ecological questions, the hypothesis that wolf research questions would have shifted over time from population ecology to social behavior was not borne out in North America, although it was to some extent in Europe where there was more concern with censusing and ecology in the 70's-80's and howl studies about social behavior and communication emerging in the 90's-2000's.

Analysis and Predictions

Most of the questions being asked about wolf howls have been around since the beginning of howl research. People ask when, where, and why wolves howl; what howls can tell

us about taxonomy; how we can use howls for population monitoring and management; and what information howls contain. Most of the same questions continue as methods get more technical and are borrowed from other areas of bioacoustics research. The only ‘new’ questions were about information theory and complexity, and those were also asked about wolf howls only after they’d already been asked about communication in other species.

The question of whether wolves have different howls with different meanings was asked by the Theberges in 1967, but their methods of describing howls were too arbitrary and the behaviors used to define behavioral contexts were socially irrelevant. The 1978 paper of Harrington and Mech was interesting because they could have investigated the meaning of specific types and structures of howls, but they failed to ask that question despite seeming to have all the relevant pieces. They recorded howls in a variety of physical and social contexts (at kills, at rendezvous sites, from dominant individuals, from pups, from lone wolves, etc.) and had access to the spectrograms (looking at howl durations and frequencies on the spectrograms is how they identified the age class of howling wolves). Even more importantly, they almost stated the question and the fact that it had not yet been answered: they did not assume that the meaning of howls was restricted to the presence or absence of howling plus whatever information a receiver could gather from the context, as some later papers did. Instead they acknowledged that “whether the structure, pitch or harmonic emphasis of a wolf howl conveys specific information is unknown”, which was why they kept the amount of variation between their stimulus howls as low as possible. The question was there in the background and they had the sonagrams and context data that could have been used to answer it, but the only howl variable the paper discussed (aside from those used to determine age class) was response rate. While it is true that

all their howls really from one context (responding to what sounded like one or two unknown intruders), there could have been differences between howls related to general interpack agonism and howls related to defense of a resource or site. The authors could have compared features of the spectrograms from some context variations without having to collect any new data. They acknowledged the possibility that howl structures could convey specific meanings, but they were not motivated to ask what different howls mean or what aspects of howls might carry specific information; they only asked when howling was used and what it seemed to be used for. This is in contrast to Palacios et al (2007), where their dataset was overwhelmingly dominated by one behavioral context and howls recorded during spring and fall were lumped together. This data could not have been used to compare howls from different contexts or seasons, although the authors note that it would be interesting to investigate whether the howl types they identified were functionally distinct.

The first study that attempted to look at structural differences between howls in different contexts was Harrington's paper on howl structure and territorial responses to simulated intruder howls. While Harrington (1987) discussed a novel question within published wolf research, the theory that gave rise to the question and the variables in howl structures which Harrington decided to look at came from a ten-year-old paper on a phenomenon found in various birds and mammals combined with a method of eliciting howls already common in other studies in the SNF. Morton (1977) reported that in the short-range vocalizations of many species, vocal qualities that make the signaler sound larger (low frequencies and noisiness) are found in aggressive contexts while the opposite qualities making the signaller sound smaller are found in

friendly contexts. Close proximity creates a strong selection pressure for these rules in most cases because it is especially dangerous to misinterpret a signal's aggressiveness level at close range, but Harrington showed that in wolves even their long-range vocalizations are affected (as Morton predicted for some social mammals). This study would not have been possible in captivity, where normal territories do not exist. It occurred at a time when the research team in the SNF had already solidified their method of eliciting responses; it was available as a tool to apply when asking if wolf howls followed Morton's M-S rules or some other structural pattern related to context or semantics.

Harrington's 1989 paper includes a lot of speculations hinting toward future research questions: rallying behaviors "may" stimulate howling, larger packs may howl sooner and longer because there is more tactile stimulation with more wolves; packs "may" learn the size of other packs from past encounters or other clues and then when they hear a pack howl they recognize the pack and remember the size; the simple-structured initial howl of a chorus "may" provide the information about pack identity, deception about pack size "may" be immune to probing because the costs of investigating a territorial pack are high, etc. Even the main conclusion is really a speculation that chorus structures that hinder a receiver's ability to determine the size of the howling pack function to discourage trespassing or agonistic behavior, and that size-obfuscating qualities evolved because they benefit small packs including pairs forming new territories.

Watson et al (2018) demonstrated a resurgence of deliberately semantic questions about wolf howls. Fruitful work on possible semantic content in howls should borrow from both Watson's captive experiments and Harrington's field experiments, as well as glean as much as possible from field observations and recordings from different observed contexts.

In 1990, Tooze, Harrington, and Fentress showed that there is an objective difference between howls from different individual wolves, meaning information about individual ID is available in howls, but they did not show that wolves hear and use this information. As for how wolves identify individuals, it is possible that the objective differences between individuals' howls do not represent the most important perceptual differences—wolf brains might have evolved to process vocalizations in such a way that different variables are emphasized with respect to individual ID, or their auditory systems could be more sensitive to frequencies in howling range or frequencies modulated in a howl shape than to non-socially-relevant sounds. Playback experiments with digitally manipulated howls and non-howl sounds could shed some light on these perceptual questions; this could lead to more educated choices of sound variables to use in future analyses of this sort. Palacios et al (2015) accomplished the step after Tooze by showing that wolves can tell the difference between howls from different wolves; the next step is to find out if wolves actually use the available information to identify other wolves from their howls and make decisions based on the howler's identity.

The 2000's were marked by increasingly technical attempts to count wolves in a recording for censusing (Dugnol et al 2008) and papers framing their results as relevant for using howls effectively as a censusing tool (Gazzola et al 2002, Servín 2000). This indicates that as some North American and European wolf populations began to recover from the wolf wars, funding was going to studies that could discover effective ways to census wild wolves and assess how their recovery was proceeding. The censusing question is still relevant; a paper from 2020 used the human howl stimulus for blind surveys where the locations of packs within study areas

were unknown in order to reveal what kind of response rates can realistically be expected from surveys in areas where the movements of wolves are not tracked and their presence may not have been verified (Ausband et al 2020).

One factor holding howl research back is the difficulty of describing continuous vocalizations, especially in the context of semantic questions where discrete syntax is thought to be particularly important. Early descriptions of vocalizations were subjective impressions of the observer, followed by sonographs accompanied by subjective interpretations. Sonogram technology was made available to the public in 1945 (Radick 2007), altering the paradigms of bioacoustics when serious wolf research was in its infancy. Sonograms began appearing in papers describing wolf vocalizations in the 1960's, following studies of vocal communication in captive foxes by Günter Tembrock in the 1950's[21]. The descriptive aspect of behavioral research matured in the 1950's as the idea of an ethogram expanded from a written list of observed behaviors (sometimes with useless attempts at phonetic transcription of animal sounds) to include records in the form of photographs, video, and sound recordings (Gräfe & Hui 2020). Tembrock summarized the change: "we have to sift the available material, order and classify the diverse forms of sound so as to be able to define and characterize them objectively in the same

[21] Tembrock founded the Forschungsstätte für Tierpsychologie in 1948 and pioneered the field of bioacoustics, beginning in 1951 with an early portable tape recorder. He became an expert on mammal vocalizations and their behavioral contexts in an open captive environment. Analysis of bird and insect vocalizations was maturing more quickly than those of mammals, and in the 1960's there was still a "frightening lack of knowledge" about mammal vocalizations (Tembrock 1962).

way as was done in morphology 150 years ago. The fact that we can now preserve sounds (as we have been able to do it with organs and tissues for a long time) forms the decisive foundation for our task" (Tembrock 1962). The introduction of the spectrograph made animal sounds measurable as characters for use in taxonomic analysis and contributed to the human bias toward vocal communication, as sounds were now easier to analyze than visual and olfactory forms of communication (W. H. Thorpe quoted in Radick 2007).

It is convenient when a sonogram displays a signal as a series of separate notes or phonemes of identifiable types, because then there is clearly a sequence of discrete units in the signal. We can uncover the underlying syntax rules that contribute to how the notes in a chickadee song, which are meaningless on their own, are arranged in sequence to produce a meaningful signal (Clucas et al 2004). It is relatively easy for humans to detect combinatorial systems in animals like the chickadee, for which researchers have been able to determine that their call system structurally qualifies as an open recursive language and is computable like the syntax rules in human languages (Hailman & Ficken 1986). Human language is as productive as it is because it is a discrete combinatorial system: meaningless units combine into meaningful units, which combine with other units according to syntactical rules into larger meaningful units. If we can identify the relevant units, we can describe any discrete vocalization as a series of characters and use context to discover some of the syntactical rules that produce meaning.

Graded or continuous vocalizations like howls are more difficult to analyze. Researchers tend to recruit increasingly technical methods to describe their acoustic structures. People describe these signals in terms of the amount of frequency modulation, the slopes of frequency changes, and the number of discontinuities in the frequency. Some papers use methods that

convert a continuous signal into a series of symbols representing how the frequency or power spectrum is changing at each time slice in the vocalization (Kershenbaum et al 2017, Placer et al 2006) and image processing techniques that can describe the shape of the frequency contour (Kershenbaum & Roch 2013). Bioacoustics research has also pulled methods from human language analysis to extract phonemes from continuous signals (Placer et al 2006).

In some communication systems, vocalizations are continuous at the production level but discrete at the reception and interpretation level. When humans speak, they communicate multiple phonemes at once and the phonemes are graded together; but receivers hear it as a sequence of discrete, consecutive units. This is why humans hear speech at 45 phonemes/second, although they can't hear a series of clicks as individual sounds at 20 clicks/second. Speech perception in humans, including the ability to perceptually equate a mental string of discrete units with a continuous vocalization, is a biological feature that cannot be duplicated by computer analysis of the actual sound waves of human language (Pinker 1994, 156-159). Computer analysis of the continuous vocalizations of another species may likewise not be able to reveal an underlying discrete combinatorial system, even if one exists, without accompanying perceptual studies. Continuous vocalizations remain difficult to analyze, and the results of semantic studies on continuous vocalizations are more opaque than those of studies on species with discrete calls.

Howl descriptions become more technical over time, but continue to include broad categories or howl types such as flat and breaking, and more recently continuous wavy and breaking wavy (Palacios et al 2007). Unlike the earliest descriptions, these types are now supported by statistical analysis showing that measuring various howl attributes leads to clusters

of howls that fall into these broad types. In the 1980's and earlier, "howl types" were based on humans looking at spectrograms and sorting based on appearance alone. Kershenbaum et al emphasized the need to describe howls objectively without including variables that stand out to humans, as wolves are the target audience of howling and their perception of howl structure may be different from that of human listeners who break howls into parts based on their own auditory system biases and visual interpretation of the spectrogram. Previous papers dealing with "howl types" included human bias somewhere in the analysis, while the classification systems of Kershenbaum and Hennelly use more technical statistical methods to attempt to remove human intuitions about which howls fall into which types—although humans are still choosing which variables to measure. Passilongo et al (2017) note that the distinctions between canid vocalization types such as whimper, yelp, snarl, woof, and bark have never been classified using objective automated techniques, only by humans hearing the vocalizations and looking at their spectrograms.

Like Tooze et al (1990), this paper Palacios et al included several variables to describe howl shape, but none that describe the order in which parts of the howl occur. Wolves recognize the difference between a normal howl and the same howl played backwards (Palacios et al 2015), and using variables for frequency modulation across the entire howl do not account for differences in how and when the frequency modulation occurs. Most studies on wolf howl structure focus on general aggregate structure, where one set of variables describes the entire vocalization. This is common in research on calls with multiple simultaneous frequency components, but it does not capture much about the actual sequence of events in a howl (for example, CoFM is the same for a regular howl and the same howl played backwards). Research

on vocalizations in other species is moving toward identifying phonemes and sequences of potentially informative units within continuous calls.

In the 2000's, prairie dog alarm call research was moving away from this kind of analysis and investigating the internal structure of alarm calls. Internal "microstructures" (acoustic units within alarm calls) were found to encode information about predator species (Placer & Slobodchikoff 2004). An algorithm from the 90's (Kohonen's self-organizing map) was applied to alarm call data to sort acoustic units within the calls into categories based on the power spectra of time slices. This SOM was chosen because it was able to identify phonemes from a continuous signal of human speech. After the SOM automatically identified unit classes based on acoustic similarities and translated each alarm call into a sequence of symbols for unit types, it was found that different units and combinations of units were associated with different predator species (Placer et al 2006). While this method uses arbitrary partitioning of calls, it is likely to be accurate based on its previous performance with human phonemes. Something similar may be applied to wolf howls and other continuous mammal vocalizations in the future and could resolve the disagreements between papers about which variables of the entire howl contribute to information like individual ID and, eventually, context or content.

Systems like the self-organizing map and that used by Kershenbaum et al (2016) are designed to remove subjective human bias. The next step should be to reintroduce subjective bias into the system, but this time from a wolf perspective. A full subjective understanding of another species' perceptive abilities and categorical biases is impossible, but clues can be gathered from research on hearing in wolves and dogs, experiments on captive wolves such as the recognition experiments of Palacios et al (2015) using specific modified stimuli designed to reveal which

aspects of howls are relevant to wolves (especially if there are howl features that seem important to humans but unimportant to wolves or vice versa), and playback experiments in the wild to see how changing the features of a howl stimulus may be interpreted by listeners in terms of their responses and reactions.

Aiming for objectivity is an important step towards eliminating artificial anthropocentric categories, but the final method must be 'lupocentric' if it is to have any meaning in its social and evolutionary context. Human communication cannot be studied in terms of purely objective measurements (for example, knowing about our categorical perception of consonants and vowels is vital to understanding our speech and categorizing our sounds the way we perceive them; an objective continuum reveals the 'truth' of the sounds, but not how they behave in our communication system), and we should not expect that vocal communication in any other species is totally objective either. Future papers on howl structure will likely involve attempts to describe continuous vocalizations in a way that is objective and perceptually accurate.

Most wolf populations today exist in exploited areas; even packs that spend most of their time in protected areas like national parks and wilderness areas usually range outside of these artificial human-made borders. Many wolves are part of restoration projects or being studied for conservation reasons. Urgency and limited funding probably leads to a focus on ecology in wolf research, but long-term studies like Haber's in Denali have shown that wolf ecology is inseparable from sociality. Where management wants to treat social species as numbers of individuals "like any other animal", policy is resistant to science that reveals wolves' social natures and the ecological relevance of individual relationships (a pack's composition,

continuity, and combination of personalities and experience levels determine the pack's spatial movements, foraging behavior including predation and scavenging, and generally the success of the group and its individuals). These trends in management may be related to the relative scarcity of communication and long-term behavioral studies even in accessible places like Yellowstone, as management policy and research grants often come from the same source.

Communication is important to study for its own sake and because of its connection with sociality. Understanding communication systems as fully as possible can provide insight into group structures, the nature of relationships over time, and social cognition. Places like Algonquin Provincial Park, the Superior National Forest, and Yellowstone National Park continue to demonstrate the importance of maintaining long-term studies. All questions are easier to answer when there is information available on pack locations, pack composition and history, movements, locations of kills and homesites, and social relationships. Social and cognitive questions and hypotheses are also more likely to emerge from long observation. As wolf research continues into the 2020's, howls and other forms of communication should be studied from an ethological framework. Researchers should seek input from cognitive and perceptual psychology and approach communication with an eye toward social evolution, culture, and the possible presence of semantic content.

CHAPTER FOUR

INTERPRETATIONS OF WOLF HOWLS

This chapter will look at descriptions and interpretations of wolf howls outside of scientific papers and what they reveal. Many historians have used such descriptions as a source of information about the humans and their biases and attitudes about wolves. In addition, I will argue that if the subject is approached carefully and combined with ethological background and observation, humans' descriptions may be able to tell us something about the wolves themselves.

While William Dwight Whitney did not elaborate on the reasons for trusting the "common-sense philosophy" that humans use to make judgments about the intentions and experiences of other organisms, I will argue that just as our beliefs in other beings and things external to ourselves which we arrive at using our senses are at least close enough to reality to have survived natural selection by allowing us to behave appropriately for our own survival, our beliefs in others' mental states (and our beliefs about the content of those mental states) must have evolved to be close enough to reality to allow us to predict the behavior of others accurately enough to survive. Similarly, many of the cues we rely on are conserved across species because they are effective at communicating intentions to others and the costs of being misinterpreted mean that on a gross level they are unlikely to change without the changes being selected against: there are reasons beyond sound structure why no animal uses a whimper to indicate that they are going to attack and no animal has a quiet and slow alarm call. Our immediate impressions of another's mental state, while they are not always correct and must be checked against cues and behavior, evolved via natural selection to be as accurate as they needed to be to

keep our ancestors alive and capable of reproduction in large groups with complex social structures; they should not be disregarded completely as if they were random.

Identifying sites of vernacular knowledge creation in the past and present can reveal forgotten conclusions and new hypotheses. By looking at the interactions between cultural biases and evolutionary adaptations that contribute to folk psychology, historians and biologists can mine amateur interpretations of wolf howling and other forms of animal communication for lines of inquiry about the animals themselves.

Historical Howl Descriptions

> *Historians... have largely ignored the voices of nonhuman animals when narrating the past. Yet, all the while, wolves still howled and people heard and interpreted their calls.*
>
> –Brett Walker, 2005

Although the contexts of observation do not determine the quality of the resulting information, observations from both amateur and scientific contexts are filtered through the observer's biases and preexisting beliefs and expectations. Trappers chasing the last wolves in Colorado must have had experience with domestic dogs and been familiar with the gestures canines use for submission, but their attachment to the idea of slaying "a worthy foe" led them to interpret the wolf's attempt to surrender as a sign of fearless stoicism (Coleman 2004, 213-214). Humans dealing with captive wolves tend to interpret any crouching position as a play bow because they are expecting friendly play behavior, but wolves have been observed to use a crouch when testing bison; one captive wolf at Wolf Park, Indiana used this crouch as a test and then attacked a human in the enclosure after they and the other humans present mistook the

testing for play (Goodmann et al 2002, iii-iv). As with any vernacular knowledge, information emerges from the amalgamation of a large body of anecdotes; these anecdotes are not expected to reveal the structures and meanings of specific howl types, but they can point toward likely hypotheses while revealing something about the cultural contexts affecting their interpretations.

Andrew Balluta (1992) related an Inland Dena'ina story about how humans interacted with wolf howls: "In the past, when people were short of food and they heard a wolf howling, they went to where the wolves had been consuming game and took the portion of the meat which had been left behind. The Dena'ina believed that the wolves had notified them by howling that there was food there and had deliberately left part of their kill for their brothers, the inland Dena'ina". The Hidatsa use an invitation song derived from a howl type that wolves were said to use after making a kill "to call the other wolves, coyotes, foxes, and magpies to the feast" (Lopez 1978, 104; Bowers 1992). Plains Indians historically respected the wolf as "a provider for the larger community" of carrion eaters as well as for their own families (Lopez 1978 103). It is unlikely that wolves use an invitation howl to deliberately attract scavengers to their kills (they can be tolerant of ravens, magpies, and smaller canids feeding on the same carcass but will also chase them away), but this song may have ultimately been based on a howl type used to summon packmates to a carcass or to reunite a dispersed pack after a hunt. These signals would be intercepted by individuals other than the intended recipients interested in locating a kill. This mainly shows a historical association and what wolf howls, or perhaps specific food-associated howls, mean to scavengers; it also implies that humans occasionally scavenged from wolf kills in the past. These humans may have attributed a highly generous nature to wolves based on their

ecological importance for scavengers. When wolves were exterminated from Yellowstone and overpopulated elk died of starvation in winter, countless carcasses went to waste because scavengers had relied on wolves to rip open the skins; without wolves, the ravens could only eat the eyes (Doug Smith talk 2018). Ravens are attracted to wolf howling and use it to locate carrion (Harrington 1978); playback studies could determine whether some howl types are more likely than others to attract ravens; these would be candidates for meanings related to food or summoning pack members.

In his 1850's mountaineer narrative, James Capen Adams explained that wolves eat in silence but "as soon as they have satisfied themselves, they usually set up a concert of howls, which is anything but pleasant." Adams talks about this wolf encounter while on an expedition in which he captured a grizzly cub which he trained to accompany him on hunts. He continues: "It is indeed a horrible noise, the most hateful a man alone in the wilderness at night can hear. To a person anywise low-spirited or melancholy, it suggests the most awful fancies, and is altogether doleful in the extreme". After a digression about how he was moved by the frightening and melancholy sound of "the lugubrious howl of a pack of wolves", Adams quickly returned his narrative to a place of mastery over the wilderness by invoking the cowardly-wolf trope and the fact that he had a gun: "I was glad to put the cowardly rascals to flight by sending a ball after them" (Hittell 1861).

In 1833, a "mad wolf" story that took place in the Green River area near Yellowstone describes a rabid wolf who had attacked the camp of some fur traders. The wolf howled near the camp at night and ended up biting a bull and a trapper, both of whom were left behind as they

had “gone mad” (Walker 2005, 111). While rabid wolf attacks were always rare in America compared to Europe, more stories of rabid wolves appeared in the later 1800’s, heightening the fear with which humans responded to howling.

In 1893, photographer and rancher Evelyn Cameron moved to Montana from England. Her diaries from the next two years include encounters with wolves, coyotes[22], and howling. She wrote about selling wolf skins and getting bounty payments for coyotes, poisoning pups at a den, chasing wolves with dogs and horses, encountering traps, finding poisoned carcasses and dead canids killed by poison, and talking about wolves and coyotes as if they were standard prey species for humans. Cameron and her associates encountered wolf tracks and vocalizations more often than they saw the wolves themselves. They heard wolves “howl dismally” (a phrase Cameron repeats several times), heard coyotes howl at night and in the morning, and imitated the coyote’s howls well enough to confuse domestic dogs. Humans setting baits kept up a “howling conversation” with their quarry. Each day in the diary starts with a summary, and one encounter summarized as “heard lots of big wolves” involved overhearing an exchange between a pack and a separated member, and possibly another pack further off: “I sat on ground waiting with horses.

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[22] Cameron speaks of coyotes, big wolves, small wolves, grey wolves, and grays; but “big wolf” is a common phrase whenever she talks about wolves or their tracks. She even describes wolves as “big” without seeing them, based only on their howls. She may have been guessing individual sizes based on howl frequency, or she may have been using ‘big wolves’ to distinguish them from coyotes. In 1850, bounty laws in Utah referred to coyotes as “small prairie wolves” and wolves as “large mountain wolves”. Eventually the term “prairie wolf” was entirely replaced by coyote (Coleman 2005, 183-186), but there may have been overlap around the time of Cameron’s diaries. In the 1860’s, wolf bounties in Montana were higher than coyote bounties, but both were included under the general category of “wolfskins” (Stuart 1866-1867). In one entry, Cameron describes an encounter between a dog and an animal which she labels a coyote twice and a wolf once in the same paragraph. Later some sheep are eaten by “wolves or coyotes”, which becomes just “wolves” a few sentences later.

Suddenly big grays began to howl so low & deep their last notes, an old one off by himself replied, about 12 more howling. They came closer & closer, until they must have been about 100 yds off, then turned off away & howled in the distance" (Cameron 1894).

A Custer County centennial history, published in 1990 and covering 1889-1989, focuses on the stories of individual humans. Wolves and their howls appear as part of the historical backdrop. A phenomenon Coleman (2004) described in Utah occurred in Southeastern Montana as well: wolves were eradicated and then revived as frontier storytelling devices to symbolize the wilderness and the hardships that colonists endured for the sake of civilizing the west. While these stories denigrate wilderness as incomplete and idolize the tamed country as the final product, they also regard colonists as a part of the final product. The preface to the Custer County history reads: "These historical events were all steps in the civilization of Custer County. They furnished the backdrop for the lives, adventures, and progress of its people. The adversities encountered produced the kind of person who became the pride and joy of this country" (Jones 1990). This also reveals nostalgia for the adversity which those who encountered it aimed to eliminate, and echoes some of the talking points of Theodore Roosevelt's time regarding wilderness and wilderness recreation as instruments for personal growth.

Its description of wildlife in the county places wolves "in the past". The "pictorial history" section places wolfers posing with traps alongside buffalo hunters, Cheyenne camps, and military photos. Frontier stories included wolves to demonstrate the hardships of colonizing the wilderness: "While he was building the house [in 1913], five wolves came over the hill, and the big male wolf killed his bull". Some of the hunters and trappers discussed in the book were dedicated wolfers while some targeted wolves opportunistically: on hunting party "changed their

avocation from buffalo hunters to trappers of wolves and beavers, as there was no sale for buffalo hides" during the winter of 1876-7. Around that time, trapping wolves and coyotes over the winter was also a job for enterprising teenagers. The childhood of one Bessie May Williams was described with wolves as part of the auditory background to a quaint, historic hardship narrative: she "was born February 24, 1888, in a dugout in West Texas" and "went to school in a horse drawn two-wheeled cart and could hear the grey wolves howling in the distance". Another subject, born in 1907, included howls in a list of historical entertainments: "in our younger days, listening to the wolves and coyotes howl, Mother reading to us at night, Saturday night dances, rodeos, picnics, swimming, riding on roundups, brandings, helping drive the fall beef herd to Benteen and later Colstrip, and visiting were our activities and recreation."

Fred Hardesty, remembering the 1920's (when some of the hunters mentioned in the book became government trappers), tied wolves and harsh winters to nostalgia when he said that "wolves and coyotes were more than plentiful in those days and I did a lot of trapping. Some of the winters were quite severe at that time; minus the modern conveniences of this day and age, but an expression we hear quite often, "The good old days", was ever so true." Wolves were on their last legs in Montana by that time, and the sighting of a pack during the winter of 1917-18 was notable and the last time a full pack was seen in the area. Interviewees who lived on a desert claim in the late 1910's-early 1920's "told of hearing the wolves howl in the winter time at night. This was about the end of wolves in that part of the country" (Jones 1990).

Fitting with the general colonial narrative, the way the Custer County history talks about Indians is similar to the last wolf stories. The interviewees were once afraid of the Indians, but not anymore because by this point they were doomed; like wolves, stories of Native Americans

which the settlers considered scary at the time are related with the phrase “those were the good old days”. One who was there “to watch the soldiers bring in the Cheyennes who were just off the war path” described the Cheyenne men, women, and children as a “howling mob”.

The niece of a wolfer in Musselshell County in the 1800’s, describing her mother moving west from Detroit in another county history, said “some of the things she feared in this new land were the long-drawn howl of the wolves, the scream of mountain lions, snakes, Indians (who never came), and strangers who might stop during her husband's absence”: the threat of the wilderness and wild predators was expressed in their voices (Hougardy et al 1974).

Wolf howl descriptions from Japan during and after the Meiji period resembled those of the American West. Travelers told the same kind of ‘surrounded by wolves’ stories as American colonists. Rabies and famines caused the Japanese image of wolves to change from ‘mostly benign’ to ‘always dangerous’, and the success of poisoning campaigns imbued wolves and the sound of their howls with nostalgia (Walker 2005, 97-101). Shiga Naoya’s 1920 story “Takibi” shows a nostalgic view of the war on wolves reminiscent of the Utah stories Coleman analyzed in *Vicious*: people remembered the past as full of danger, wolves, and wilderness; telling stories of this past from the perspective of a civilized present turns the fear of wolves into nostalgia for the hardships of bringing modernity to a wild landscape. In “Takibi” an innkeeper says that there is no longer anything scary in the mountains—no dangerous animals or supernatural creatures—and then brings up the extinct wolves: “When I was a child, often we just heard their distant cries. Hearing their cries in the middle of the night, I remember that a lonely, uneasy feeling came over me” (Walker 2005, 97).

Euro-American howl interpretations shifted from fear-based to anthropomorphic dramatizations with the rise of the last-wolf story. To fit the last wolves into the noble savage archetype, storytellers combined the sound of howls with projected emotions like rage, bloodlust, loneliness, yearning, threat, invitation, defiance, and vengeance.

Carhart and Young's book of last-wolf stories, *The Last Stand of the Pack* (1892), is full of howls interpreted as lonely and warlike. Old Lefty's howls are repeatedly described as a "challenge" to "invaders" and "intruders" in his territory, once a "bellowing challenge". Another wolf "bellowed defiance" in a "half bark, half howl" challenge. It is clear that the cowardly wolf trope is dead when Lefty is fighting a trap: "bellowing his rage… no fear, no cringing, only mad hate, the spirit of the renegade, mastered him… he voiced his hatred while timid woods dwellers cringed in their coverts at that fighting, blood-lusting cry".

Carhart describes howling as an instinctive release of emotion that can only sometimes be suppressed. One wolf, overcome by emotion and instinct, "Finally giving into the irresistible force, she raised her head and in trembling crescendo sent forth the cry for the pack" with "a new challenging command in the call". Later this wolf uses howls as weapons in a war with humans: "Howl against howl she hurled at [the hunter]. In him she saw the force that was warring on her kind. Instinctively she knew that here was the man that was making her life one succession of pitfalls, poison, snares"—in this context the howls reinforce the idea that wolves and humans are enemies because of circumstance (also stated when one of the hunters mentions that "renegade" wolves always seem to be those crippled in some way by traps or guns and then "go bad"; and in stories where the wolf is involved in the war because it has a grudge against humans for killing

its mate or pups). Carhart says that howl, called both “her language” and “her mad cry”, was full of “venom, hate, vindictive, passionate anger that she carried against man”.

Whitey of Bear Springs Mesa “lifted up his head, threw back his ears, and from his throat sent forth the call to the pack”—a more realistic depiction of how howls are used, although Whitey is described as a “king” who “mustered his following” using vocalizations. More wolves in the book also howl to summon others and express confidence that their packmates will come when they howl for them. Rags the Digger is moved to howl by strong, conflicting emotions; after stifling the urge to howl while stalking a human, he encounters a trap and is filled with so much hatred of man that he “bellowed forth a great, full-lunged wolf howl”. This story ends with a suicidal acceptance of defeat, but while colonists described surrendering wolves as cowardly (Coleman 2004), Rags does it with “regal bearing”. Other wolves are described as royalty and given traits of a human monarchy. When Unaweep “bellowed forth that pack call, the wolf howl summoning to the hunt”, it was “the call of the king wolf, very rarely voiced by females”—while real wolves readily follow female leaders, Carhart’s female king was “contrary to wolf law”.

Carhart described the wind as howling when it is there to scare the humans in the story, who felt “a creepy feeling along his spine” and “a fear of the wilderness”. Many of the wolf howls in the stories echo from cliffs and canyons for dramatic effect. Carhart gives howls a lot of frequency modulation when they are meant to be particularly emotional or “eerie”: these are “trembling” or “wildly quavering, the breaks with blood-chilling echoes”.

A typical last wolf story appearing in a Lewistown newspaper begins with howling to set the tone: “Never again will be herd [sic] from the hill-rim the soul thrilling voice of the white monarch of the wilds” (Elva 1930). This story goes on to include every last-wolf trope there is:

the “outlaw” was old, white, alone, had a history of evading hunters and traps, has a leg wound from being shot in the leg, is described as “a cunning strategist, cruel and brutish following the death of his mate in a trap a few years ago; the big wolf became still more devilish murderous”, and final actions were twisted into a noble savage archetype: “As he lived, bold, courageous, arrogant, flaunting his contempt for man and beast alike, - so he died, head up, facing the rifle unflinching and fearless.” While the story clearly takes the hunters’ side, it also glamorizes the wolf and his “soul thrilling voice”. By this time, wolf killing was more of an adventure than a practical part of settler life; the humans who went out to shoot the wolf were described as “unable to resist the glamorous call of the wild”.

Many people read stories like these and assume they can reflect only the people who wrote them. Because of their socioecological similarity to humans and equivalence with the concept of wilderness, wolves are consistently treated as a canvas for humans to project onto. Some writers merely observe this while others embrace it. Peter Steinhart said that “each of us invents our own wolf” (Steinhart 1995, 337). We all invent everything to some extent as we can only interact with the world through our senses and schemata, but humans’ mental representations of wolves seem to be accepted as more invented than those of other animals.

Barry Lopez describes this phenomenon without always keeping an eye on ‘the real wolf’, which potentially makes it easy for readers to forget the biological relationships behind the stories: “The wolves of the plains were, of course, whatever one wanted to make of them. Thus the howling wolf was the Pawnee’s spirit talker, the missionary’s banshee, Maximilian’s music, and the lone traveler’s sleepless nightmare” (Lopez 1978, 177). Jon Coleman (2004)

attempted to bring wolves' voices back into the picture by keeping track of what wolves were likely communicating to each other and attempting to communicate to colonists while he traced the colonists' wolf image and the features they gave to the wolves in their stories.

In "Thinking Like a Mountain" (1949), Aldo Leopold described a howl as a "deep chesty bawl". He also used a description that would not have been out of place in a last-wolf story: an "outburst of wild defiant sorrow, and of contempt for all the adversities of the world".

> To the deer it is a reminder of the way of all flesh, to the pine a forecast of midnight scuffles and of blood upon the snow, to the coyote a promise of gleanings to come, to the cowman a threat of red ink at the bank, to the hunter a challenge of fang against bullet. Yet behind these obvious and immediate hopes and fears there lies a deeper meaning, known only to the mountain itself. Only the mountain has lived long enough to listen objectively to the howl of the wolf (Leopold 1949).

Leopold's famous essay lists what the wolf's howl means to deer, coyotes, pines, humans of different kinds, and the mountain, but fails to realize that the true meaning of a wolf's howl is whatever it means to wolves. He treats the howl as a feature of wolves, effectively a symbol for the concept or presence of wolves, rather than a signal that functions to communicate something. Leopold uses howls as a proxy for wolves themselves, which many writers do (especially in forested areas where wolves are easy to hear without seeing), but this may have cause people to lose sight of the biological reason why wolf howls exist: wolves evolved to howl because of how it affects other wolves and the only objective meaning in a wolf howl is the meaning it has to its intended recipients. If ecosystems had opinions, Leopold's mountains would have a "secret opinion" about wolves as a key predator in the ecosystem, but even recalling the "green fire" in the dying wolf's eyes, Leopold failed to perceive the wolf as a fundamentally social animal who howls not because he wishes to reassure the ecosystem of his presence or reveal fundamental

truths about ecology to eavesdropping humans, but because he intends to communicate a certain message to others of his own kind.

This is not to take Leopold too literally, but to point out that even with an ecological consciousness, humans can easily fall into the trap of seeing wolves as either isolated individuals (as Leopold thought about the dying wolf with green fire in her eyes, as the last-wolf stories and their cultural residue teach people to think of "lone wolves", and as visitors to YNP think of individual wolves who have become famous with their personal life stories and dramas) or populations on a purely ecological level (thinking about populations as nothing but a number of wolves to be balanced with a number of elk; leading to statements that one should "manage wolves the same as any other animal" and failure to notice that pack structures and specific combinations of individuals are what govern wolf life, success, and overall behavior rather than a single number for population size). The real wolf is above all a social species, and the more one projects onto wolves and their communication, the less one is able to notice the gaps in their knowledge about how wolves relate to their environment ecologically and socially.

Steinhart lamented the demise of human culture united by shared stories and a shared spiritual view of wolves. "Each person you talk to sees a different wolf. One wolf strikes fear into the heart, another is companionable and playful, another rapacious and another knowing and sympathetic". Listing various cultural influences that talk past each other or collide in the village of Fort Chipewyan, Alberta, he includes different Indian groups, Catholics, industrialism, and "a smattering" of ecology (Steinhart 1995, 336). While science is not separate from culture and the scientist is not immune from creating his own wolf, the ethologist's wolf can be expected to be closer to the real wolf than the Catholic's allegorical wolf or the rancher's boogeyman wolf.

Constructing a wolf image based in ecological and evolutionary context, social and cultural dynamics, and long-term observation (while keeping sight of vernacular and indigenous knowledge based on generations of earlier observation) is the best tool we currently have when it comes to trying to understand wolves as they are. Writers who accept humans projecting onto wolves as inevitable should use it as a source of information about human culture and wolf-human relations in different places and times, but avoid embracing projection or assuming that humans are incapable of seeing wolves as anything but a mirror. If no human can approach wolves with a blank slate, they can still endeavor to identify which impressions come from humans and which come from wolves themselves or from a shared evolutionary history between social mammals; humans can build up their image of wolves using as many pieces as possible that come from wolves themselves in order to approach an image of wolves as they relate to their environment and each other.

Wolf howls seem to elicit a deep emotional reaction in humans, which cases the listeners to rush to interpret the howls and associated emotions. Whether they see it as wolves talking to the spirit world (Lopez 1978, 103) or an expression of their own loneliness in a new landscape, humans have a visceral reaction to howls that tempts them to interpret them in their own context before examining what they mean in the wolf's repertoire. Comparisons of howls to music and song likely stem from this emotional response (as howls are not structured as songs like those of birds or whales). In 1814, a surveying crew in Ohio had what Coleman called an "interspecific conversation" with wolves, who howled at night and responded to the humans making noise. The surveyor said: "they always, in passing, saluted us with a specimen of their music."

Contemporary descriptions of howls that call them music or song tend to be positive, especially in contexts where wolves were extirpated and then recovered or were reintroduced ("It was a song not heard in the Smokies for one hundred years", DeBlieu 1992; "coyote howls surrounded us like a sonata", Askins 2012), but this was not the case in earlier descriptions. Settlers in 1818 said they were "serenaded by a pack of hungry wolves" as they hid in a cabin. A Mormon traveling on the Great Plains in 1848 said that "the music in the wolves' choir seemed to introduce in me a desire to feel a little religious"; another group was "regaled all night" by howling wolves. Howls were described as both 'music' and 'noise', often at the same time, and always with a sense of fear as the wolves' long-distance vocalizations were interpreted in light of the settlers' anxieties over dominating the wilderness. In the case of the Ohio surveyors, they did not treat the howls as atmospheric background noise or as one side of a reciprocal conversation, but used the wolves' territorial response to their own noisemaking to figure out the pack's travel route and set traps along the path (Coleman 2004, 98; 163).

Elbert F. Bowman (1938) discussed the relationship of wolves to humans on an Eastern Montana ranch from about 1880-1920. He confirmed that wolves were not dangerous to humans in that country, and that "Indians called them brother" and "paid the wolf due respect for his cunning". The uses of the word "wolf" in sign language represent historical associations humans had with wolves. These include 'I will find out', 'we saw', 'our scout says', and other phrases related to finding out and sharing information. Bowman, like many others, refers to wolf howls as music as he expresses a typical combination of nostalgia for the disappearing wolf and confidence that the wolf's demise was necessary: "Yes, the wolves are gone. Never again in my time and country will dim ghostly shapes lope tirelessly on the long ridge and across the sage

flats. Never again will I hear the strange savage music of their howling. I miss them, yet I would not wish them back. But if in the hereafter comes a time when we can meet as wolf to wolf and man to man I shall be glad" (Bowman 1938). A poem by Alaskan trapper Alda Orton, who was writing in magazines in the late 1930's and 40's, calls howling "wild, untamed music". But in this poem, howls elicited a more primal reaction than nostalgia or propaganda-inspired fear. "It sent / a queer shivering feeling along my / spine. It was not a feeling / of fear, you understand, but a sort of / tingling, as if there was hair on my back / and it was hackling" (Lopez 1978, 39).

Contemporary Howl Descriptions

The fear of wolves has not entirely disappeared (aside from being a large predator, the wolf still represents wilderness and 'outsideness' to modern humans accustomed to staying within city walls), but recent descriptions of wolf howling are much less likely to evoke images of the human observers cowering in their tents believing that the wolves' chorus indicates a hunger for human flesh. But humans have not returned to pre-agricultural brotherly view of wolves either. The war on wolves which made them endangered also elevated them, and modern humans hearing a wolf howl tend toward awe more than fear, malice, or familiarity.

In North America, and especially in Yellowstone after extermination and reintroduction, the sound of a wolf howling is associated with an aesthetic proxy for ecological completeness: if the wolf howl is part of the auditory landscape, the ecosystem is healthy; if it is absent, humans feel that something is missing. This tendency calls back to Rachel Carson's 1962 *Silent Spring*, even the title of which associates ecological degradation with the silence left by the absent voices of extinct animals, as well as Leopold's association of respect for predators' presence in the

ecosystem with a land ethic. Many popular books on wolves today use the presence or absence of howls in the auditory landscape to evoke the destruction or health of the land.

Historians, Writers, and Off-Duty Scientists

Popular and historical books about wolves invariably make use of howling encounters to set the scene. Lopez introduces *Of Wolves and Men* by following a wolf through a Canadian forest: "Toward dusk he is standing by a creek, lapping the cool water, when a wolf howls—a long wail that quickly reaches pitch and then tapers, with several harmonics, long moments to a tremolo. He recognizes his sister. He waits a few moments, then, throwing his head back and closing his eyes, he howls. The howl is shorter and it changes pitch twice in the beginning, very quickly. There is no answer." Lopez carefully describes the acoustic properties of both howls without attempting to assign semantic or emotional meaning to the differences. He then describes the wolves approaching each other and using short-distance vocalizations in a greeting—"when they come together they make high squeaking noises", encircle and touch each other, and finally walk off (Lopez 1978, 11-12). Brett Walker includes his reaction to wolf howls in the beginning of *The Lost Wolves of Japan* with the voices of Yellowstone wolves standing in for the extinct Japanese wolves: "I have heard wolves howl on many occasions, usually when the sun begins to set and the temperature begins to drop in the Lamar Valley in Yellowstone National Park. Darwin would have been delighted to learn that it indeed raised every hair on the back of my neck." Walker also uses the absence of howling in post-wolf-war Japan as an ecological warning about extinction along the lines of *Silent Spring* and imagines an affective response to the howls of Japanese wolves while they were alive: "the cries of wolves that eerily split the crisp winter

nights of Hokkaido more than a century ago are only one voice in a chorus of voices warning us of the silent future that surely awaits us." (Walker 2005, 12; 23).

Jon Coleman's 2004 book *Vicious* was a history of the human-wolf conflict in America from the intersection of folklore, history, and biology. Coleman makes a case for the conflict stemming from cultural differences as well as ecological competition: wolves and Euro-American colonists were both carnivores, but only the colonists had a concept of prey ownership. While wolves will defend a kill or a territory (and by extension any prey animals that happen to be in their territory at a given time), the colonists considered certain prey animals to be their property regardless of where they roamed. Coleman brought aspects of wolf biology into his history in order to open up more lines of explanation for events involving wolves and humans that had often been explained only in human terms. Wolves and humans evolved with compatible social systems because of selection for similar social environments, and both possess the ability to adjust to changing environments using cultural change, which is faster than natural selection (although humans are more flexible than wolves).

One of Coleman's central arguments is that wolf social politics appear volatile and intimidating to humans because of the species' different lifespans; because humans cannot keep pace with the social order of 2-year generations, "wolves and people inhabit overlapping but fundamentally different lifetimes" (Coleman 2004, 150-152; 162). While this point about generations and lifespans is true, much of the observed sociopolitical volatility in wolf packs may be a product of human exploitation. Long-term studies of wolf packs in Denali, while certainly not free of politics, revealed that when humans did not hunt wolves or otherwise

interfere, packs are more stable extended-family structures with cultural continuity and consistent use of the same territories. Elsewhere, unexploited populations yield complex packs (consisting of more than parents and young of the year) which are more successful at hunting, territorial defense, and cultural transmission of knowledge.

When Coleman talks about howls, he discusses how Euro-American settlers arrived on a landscape populated by wolves and the howls they use to promote group cohesion and maintain spacing between packs. The settlers intercepted these signals—messages sent by wolves and intended for other wolves—and, in their paranoia about their vulnerable presence in an untamed frontier, interpreted howls as threats directed at them. While Coleman's main thesis about the way Euro-American settlers intercepted messages and projected their own emotions onto them is convincing, he couches it in false assertions about the nature of non-human communication in general: "Humans have cloaked these [territorial] markers in the language of science and fantasy. But wolves neither perform a cost-and-benefit analysis nor express a dreamy longing when they howl. *Like all forms of nonhuman animal communication* [emphasis added], wolf signals are simple, clear, and rigid. Wolves communicate through basic dichotomies: present or absent, approach or retreat, fight or flee, trust or fear. They have no talent for nuance or novelty" (Coleman 29). He wants to set up a contrast between human language and the fictional monolith "all forms of nonhuman animal communication" on which to blame the settlers' misinterpretation of howls, invoking an echo of Max Müller's uncrossable Rubicon: human language is positioned as being unique or having unique qualities that appeared suddenly instead of evolving gradually and accumulating complexities over time.

In real life, of course, wolf communication is full of nuance and grey areas, and cost-benefit analysis or something like it must be employed at least some of the time when wolves respond or refrain from responding to howls according to their group size and location relative to resources; Coleman later acknowledges cost-benefit analysis when describing Fred Harrington's findings that wolves "howled from a position of strength" (Coleman 2004, 28). Wolves would be unable to navigate their own social groups if their signals were binary or dichotomous. Wolf signals exist on a graded continuum within and between call types such as growls, whines, and howls; this allows them to convey nuance and communicate a wide variety of emotions, motivations, and intentions. Frequency, amplitude, speed, and magnitude variations in various animal signals often express the level of urgency associated with the signal; a dichotomous communication system in which animals could only communicate maximal urgency or no urgency at all would be inconvenient to almost useless in many species as it would cause prey animals to either waste energy responding to every alarm call as if the predator were maximally dangerous and maximally close or sacrifice vigilance by not calling attention to predators that were less dangerous or farther away. It would also cause social animals like wolves to get into countless potentially fatal fights with packmates because there would be no way to express intermediate motivational states like mild irritation. There would also be no intermediate signals, generally used to communicate indecisiveness between possible courses of action. Most social animals would not be able to live in groups without the ability to express ambiguity, indecisiveness, different levels of arousal, and other forms of nuance. Coleman must know this since he had to read about animal communication in order to write his book (and presumably he has met a domestic dog at least once in his life).

Coleman tries to make the point that the true nature of wolves is neither scientific nor romantic: those are both human projections of themselves onto the wolves based on the humans' emotions, cultural positioning, and what kind of scientific paradigms they view as objective at any given time. In his introduction he echoes Tinbergen's ethological drive towards understanding animals for their own sake and credits recent wolf studies with having "gone a long way toward understanding wolves as wolves rather than as figments of human imaginations" (Coleman 2004, 3). Wolves in reality are simply themselves, defined by ecological and social relationships that do not depend on the images humans generate, but Coleman largely replaces one human projection with another—one that wouldn't have been out of place in the mid-19th century, which is strange for someone whose alleged goal is to give wolves agency in the colonial history of America.

A year after *Vicious* examined wolf-human relations in the American West (primarily Colorado and Utah), Brett Walker published *The Lost Wolves of Japan*, which gives a similar treatment to the now-extinct Japanese wolves. Walker's goal was similar to Coleman's in that he aimed to add wolves back into the narrative as historical actors and glean some information about the wolves' actions, positions, and intentions from what was recorded by humans during the extermination campaign. "As a historian trying to piece together the whole picture, these traces of wolf voices, so lifelessly recorded in archival documents, still haunt me. I can never feel that I have done justice to this topic without having tried to comprehend what those voices said." He argues that wolves are historical beings because they have culture and historical lives of their own and are part of the "greater cultural and ecological milieu" that defines the shared histories and natural histories between themselves and humans. He talks about using emotional

expression as a text to give voices to nonlinguistic animals the same way archeological artifacts are used to give voices to nonliterate humans in history; investigating the traces of animal expressions in the historical record "to give animals greater agency in historical narrative" (Walker 2005, 13). His intention is to include wolves in the history as cultural beings ("capable of passing down learned, adjustable behavior, often in the form of what we recognize as local cultures or traditions") worthy of being studied with the kind of historical approaches used when studying humans (Walker 2005, 105).

Despite his purported intent, Walker still spends most of his book explaining how wolves were represented in the historical record based on how they fit into various human paradigms. Coleman does the same, and tries to interpret some wolf behavior in contradictory and overly humanlike ways. While he first claims wolves have no concept of ownership, he also says that wolves attempted to communicate with human settlers as they would with other wolves and directed some of their territorial howls at the human predators (Coleman 2004, 97-98). It is unknown whether wolves direct their howls at heterospecific receivers, even if heterospecifics intercept or eavesdrop on their howls to glean information about the wolves' numbers and location. After the reintroduction into Yellowstone, wolves competed with the coyotes which had boomed in their absence and killed them when they had a chance. Now the territories of Yellowstone wolves and coyotes overlap and competition mostly occurs around carcasses. In a Michigan study, coyotes did not change their response rate to playbacks of coyote choruses based on whether they were inside or outside of wolf territories. The same study also used lone wolf howl playbacks and coyotes responded to them as well (Petroelje et al 2013). Territories do not appear to be divided among wolves and coyotes, but the species can overlap and probably

disregard the territories of each other; the possibility that wolves would treat humans (especially humans engaging in the recent development of animal agriculture) the same way they treat other wolves in terms of territorial exclusion is unlikely.

Coleman tends to negate the agency of animals or misrepresent their ecological positions even while trying to incorporate them as historical actors. He equates humans killing wolves to an act of depredation to which the apex predator was not able to respond, but humans did not regularly prey on wolves (an argument could be made for the fur trade, but the war on wolves was an example of violence rather than predation). Coleman, like Grandin, is aware that depredation is an instance of foraging, not violence; yet he characterizes the war on wolves as predatory (Coleman 2004, 74) where he should have compared it to instances of violence within a species or competitor-killing within a guild—and the rest of the book supports the claim that humans killed wolves out of spite or violence and competition within a niche. He also ignores learning in several instances. In one case he claims that natural selection on location preference is responsible for deer in Minnesota spending more time in the buffer zones between wolf territories (Coleman 2004, 80). This mechanism would act far too slowly to account for behavioral changes that could be easily explained by learning, especially given the constant fluctuation in pack sizes and border locations. The selection would be for learning speed.

He ignores learning in wolves as well when he writes as if they are born knowing what prey to chase instead of learning it from experienced adults. Long-term observations like Haber's show this learning process as well as what changes when young wolves are left to their own devices; short-term observations in places like Yellowstone can also show how young wolves will chase after healthy elk that adults would ignore unless more vulnerable prey was

unavailable. Coleman also forgets one of the most basic facts about wolf packs, which is that they are mostly composed of immediate family members and intrapack behavior is driven primarily by kin selection—he says nonmating pack members "shoulder the costs" of reproduction "without receiving any of the benefits" (Coleman 2005, 155), even though most of the pack members share at least 25% relatedness with the new pups, if not 50%.

Walker confuses artificial selection (purposeful selection by one species for traits in another which would benefit the species doing the selecting) with selection that happens to involve humans; claiming that anthropogenic changes in the environment applied artificial selection on wolves. This is because he defines "artificial forces" historically as "influences emanating from the human-fashioned world" (Walker 2005, 47-55); but to apply this usage of "artificial" to artificial selection in biology makes the term useless—one might as well say that cheetahs have artificially selected for gazelles that run faster (when in reality, if cheetahs were to impose artificial selection on gazelles, they would select for slowness) as to say that humans imposed artificial selection on wolves simply by changing the environment with no intentions regarding wolf traits. These lapses in biological reasoning cast some doubt on historians' interpretations of wolf history and behavior as recorded in primary documents.

Both Coleman and Walker speak of a war *between* humans and wolves rather than a war waged *on* wolves *by* humans—Coleman suggests that wolves directed territorial messaging at humans; Walker says that ecological conditions in Japan caused the competition between humans and wolves to become 'warlike' on both sides (Walker 2005, 226). While Coleman is sometimes successful in disentangling settler anxieties from the wolves' actual actions (wolves do not drive their prey by howling when they hunt, but travelers heard howls and felt surrounded

by predators; wolf activity and howling peaks around sunset when humans are going to sleep and are easily frightened; etc.), but in the end he only replaces the settlers' ravenous outlaw with yet another fictional wolf.

These historians miss some important biological points, weakening their ability to accurately describe the historical and ecological positions of wolves. Coleman in particular misrepresents biological facts about wolves and the opinions of scientists. He claims that evolutionary biologists never study the decisions of individuals, despite ethologists and other behavioral scientists who study conscious decision-making as an aspect of behavior and cognition under natural selection. He also says "no theorist believes" that affection can be a cause for altruism, and that then "animals do not behave altruistically in the sense humans understand the term". While it may be true that there is no such thing as pure altruism, that conclusion would apply equally to all species; humans would not be excluded. He also confuses the evolution of behaviors with the decisions some organisms are able to make about their own behavior. "No thought, feeling, or decision propels evolution. Evolution drives itself" (Coleman 2005, 158-159) is an empty statement intended to sound insightful— all conscious behaviors must be driven by thoughts, feelings, and decisions to some extent; the thoughts, feelings, and decision-making abilities evolved through natural selection because of the ways they allowed organisms to respond to their physical and social environments. One could say that evolution drives itself in the sense that any evolutionary changes become part of the selecting environment, but Coleman used this phrase to minimize the contribution of wolves as agents to the history of wolves and humans in North America, the opposite of what he set out to do in *Vicious*. A final removal of agency comes in Coleman's conclusion, where he posits a historical reason for wolf

reintroduction which treats animals with their own lives as historical monuments existing for the benefit of humans as "living reminders of the legacy of colonization" that "embody an unbroken history of conquest" (Coleman 2004, 234-235).

Coleman and Walker make an important point about animals in history, specifically cultural animals like the wolf, and both books reflect a growing awareness in the mid-2000's that historians needed to be able to treat nonhuman animals as actors rather than artifacts. Much of wolf life revolves around social groups and cultural learning, so the study of wolves should include cultural history along with ecological history. Methods developed for studying humans (historical, sociological, and anthropological) should be applied to cultural animals such as wolves. Just as sociobiology brought biological methods into the study of humans, a move toward animal history or cultural studies would bring history and sociology to the more social and cultural animals. Where Coleman and Walker proposed this shift but then stuck to the human side of wolf-human relations, future projects should include extensive field observation over multiple generations of the same packs (like Haber's in Denali). Archival work documenting humans' reactions to and interpretations of wolf behavior over time are part of the picture, but these pieces as described in books like Coleman's and Walker's must be combined with observations of real-time cultural changes in wolf packs and study of landscapes and traces (ecology, topology, and evidence of past wolf behavior such as den sites/ bones/physical evidence of wolf-human encounters) to form a truly interdisciplinary project involving ethology and wolf-focused history.

Non-historians writing about wolves also spend a lot of time on wolf-human relations. Reneé Askins, who studied under Erich Klinghammer at Wolf Park in Indiana and later formed the Wolf Fund to assist wolf reintroduction into Yellowstone, featured howling and communication in her 2002 memoir *Shadow Mountain*. She describes humming "Doctor Doolittle" while working with captive wolf pups, and says that "the animals spoke through their roaming and their roaring, their howling and their prowling" (Askins 2002, 17). Askins is unlike many other wolf people in that she actively inserted herself into the howling conversation. Instead of listening as a spectator or imitating howls to get a response, she describes herself as howling spontaneously to express emotion or to achieve a goal, just as a wolf would. When some pups were being driven from Wolf Park to a research facility, she howled after them and initiated a chorus among the remaining wolves—they "called out in the long, graceful wail that is the code of their species". When she had to break her dog out of the pound, she located the dog by howl-and-response, using howling for exactly the purpose it evolved for (Askins 2002, 20;146).

While recording captive wolf behavior in an ethogram, Askins described learning about wolf cognition through cultural immersion: getting to know "their intelligence, imagination, sensitivity, and sophistication" while "immersed in wolf society". When describing her undergraduate work, Askins dives into the 'sense of wonder' that inspires scientists to work but doesn't have a place in scientific publications. In this case spending time with another species provided her with "insight" into otherness without the hierarchal baggage of the ladder of being. She also noted a gap between language and cognition: "it was the first time I felt the utter limitations of language, and the first time I truly began to face and fathom the capacity of another species" (Askins 2002, 15-16). She did not go on to become a wolf researcher, so when she

presents her “origin story” her main focus is on the contrast between captive wolves and the reintroduction of wild wolves which would become her main goal. What she writes about communication, cognition, and trying to relate to wolves from a place of cultural immersion (which is not possible in the wild) is still relevant to amateur perceptions of communication and some perspectives from researchers outside of and parallel to their work; as Askins describes gaining insights into wolf behavior from spending time with captive wolves more than from recording the ethogram.

The cultural immersion angle can easily become artificial and disruptive if a human attempts to integrate into a wild or captive wolf pack. Humans have tried to become part of captive packs and ended up on the losing end of competitive interactions, and claims to have integrated into a wild pack are fictionalized at best. While it is easier to have social interactions between humans and wolves in captivity, it adds another layer of being out of context. Wolves on their own don’t behave ‘normally’ in captivity, and adding interactions with humans makes observations even less extrapolatable to the behavior of wolves in the wild. There is something to be gained from the recognition that being a different species does not automatically turn you into a nonexistent observer, and that interspecies social interactions are possible and could teach you something about cognition and motivation. This is especially true between species with similar socioecological backgrounds. After all, if wolves and humans were not at least somewhat socially compatible, dogs would not have been domesticated. There is also something to be said for using anthropological approaches to study cultural species. Ultimately, however, wolves can only be understood in their evolutionary context, with some necessary but limited contributions from human-habituated captive wolves in abnormal environments.

While wolves and their behaviors are often described with emotionally loaded or carefully neutral language that changes with human attitudes toward wolves, wolf-related policies and research, the words “haunting” and “mournful” consistently appear in descriptions of howls from wolf haters, wolf lovers, scientists, and historians from the 17th century to today. When Coleman discussed Fred Harrington’s work, he used the world “haunting” of his own accord, not quoting any earlier description. A story from 1840’s Texas describes a girl who was raised by wolves and then captured by humans using “loud, mournful, and incessant howling” to call the wolves to her to help her escape (Lopez 1978, 243). While writing *Of Wolves and Men*, Lopez himself raised two hybrid red wolves in captivity and said that they “howled mournfully” in the first few weeks after being taken from their parents; he speculated that their howls were lonely as they sensed “their isolation from others like themselves” (Lopez 1978, 280). Jan DeBlieu, an author who assisted in the first red wolf reintroduction project in North Carolina, describes hearing “the ethereal, mournful howl of wolves”. Whether these words reveal a commonality between mammals in interpreting vocal affect or simply an unconscious tendency toward onomatopoeia with the long double vowels in these words possibly evoking the sound of a howl, they are some of the very few constants in wolf descriptions over time ranging from the unabashedly opinionated to the scientific. Observations of chorusing wolves lead to the conclusion that they are anything but “mournful”, but actual mourning howls are said to be longer and deeper than other kinds of wolf howls; and since howls in general are somewhat long and deep especially compared to human vocalizations, people might use words like ‘mournful’ (as well as ‘lonely’ and ‘plaintive’) because howls are long and low compared to their own

speech. Wolf howls are also commonly described as mysterious and otherworldly. Wolves themselves are said to haunt the mountains, and for a human traveler enmeshed in the inside/outside paradigm, hearing wolves howl at dusk from out of sight caused a sense of aloneness, vulnerability, and confrontation with the wild and eerie outer world (DeBlieu 1992, Coleman 2004, Walker 2005).

Writers use howling to evoke a mysterious or mystical reaction, drawing on the elusive and 'outside/otherworldly' nature of wolves as encountered by humans. When Askins was unloading a roadkilled wolf carcass with Dave Mech's team, a nearby pack started howling and Askins was made aware of how the inside/outside dichotomy was embodied by wolves in North America as much as in Japan. "This was a thrill for me, who lived far removed from wild wolves, and I was struck by the strange juxtaposition of the mystical and mundane one encounters in scientific research. The road-killed wolf lay stiff and inert… while the frigid air filled with the mysterious and beautiful howls of its living brethren" (Askins 2002, 155). In 1962, Wallace Stegner described howls in *Wolf Willow* as "faint and musical and clear" and he [human listener] might have been tempted to think of them as something not earthly at all, as creatures immune to cold and hunger and pain, hunting only for the wolfish joy of running". Barry Lopez also talked about mystical, otherworldly, and sacred impressions of wolves, their howls, and their life as predators—"sacred is not the right word, but hunting may have overtones for wolves that we cannot appreciate. We seem to sense them, though, when we speculate on the reasons for group howls after a successful hunt" (Lopez 1978, 93).

Wolf Watchers

The reintroduction of wolves into YNP in 1995 grew into a unique opportunity for researching wild wolves in a place where their population is dense and where they regularly frequent areas with sparse vegetation close to roads instead of being hidden in dense forests and mountainous regions that are relatively inaccessible to human observers. Askins described humans' reaction to wolf sightings on Shadow Mountain, bordering Grand Teton National Park, shortly after the reintroduction: "The mystery of their quicksilver presence, slipping in and out of the haze of winter frosts, the lingering notes of their howls, prompted hushed whispers and eager gossip. Everyone talked about where the wolves were, when, and who had seen them. Sightings were considered privileged information, guarded greedily and shared pridefully. Even local ranchers, suspicious, reluctant, a little resigned, showed up with their binoculars at some of the overlooks where the wolves were frequently sighted" (Askins 2002, 284). A culture of amateur wolf watching developed quickly. Yellowstone wolves have fans from all over the world, some of whom make a yearly pilgrimage to the park to watch wolves while they are most mobile in the winter. Other regular wolf watchers are people who live near the park year-round. They gather in the Lamar Valley especially around dawn and dusk, set up their scopes on the side of a road or on top of a nearby hill, and wait for the wolves to come into view.

Wolf watchers tend to travel in packs and follow interpretive rangers and Wolf Project biologists hoping for information. In turn, other park visitors (tourists and more casual wolf watchers) follow these packs. A small group inevitably becomes a crowd as passers-by pull over to ask what the watchers can see, and watchers as well as rangers let visitors look through their scopes. They gradually learn the most likely places in the topography for wolves to be found travelling or resting, and become experts at spotting (Ilona Popper, personal communication).

One wolf watcher described the group of regulars as a territorial pack. A former bear researcher agreed that the wolf people in Yellowstone are more territorial than enthusiasts of bears, birds, or any other species. Steinhart in 1995 and a wolf watcher in 2019 expressed similar hypothesis about wolf watching as a substitute for wolf hunting. Scopes are the new guns and having expensive, high-quality scope is used as a status symbol. Many people are content to "get" a wolf by finding it in the scope, but then they turn away and move to a new location or chat with the other watchers instead of continuing to watch the wolves. To be fair, wolves in visible spots during the day spend a lot of time sitting around, but many watchers and visitors get satisfaction from simply finding the wolf—seeing interesting behavior is a bonus.

Do wolf watchers know anything about howl meanings that biologists don't? So far, in Yellowstone, the answer is no. When wolf watchers tell stories about howling, they tend to focus on the presence or absence of howls and try to glean their intended meaning from the context. This could be because wolf watchers aren't necessarily listening to wolves howl with the intent of predicting their behavior, besides the reuniting of separated pack members. They find howls exciting and charismatic but don't often try to interpret them. They identify individuals by their color, size, and whether or not they are collared; much of this information is learned from interpretive rangers. Wolf watchers have not developed the kind of skill that the Nunamiut hunters had for sexing and aging a wolf from a distance; instead they ask a nearby ranger or experienced wolf watcher who can tell them who is who or whether to expect a chase or test of an approaching herbivore. Information about the packs, individuals, relationships, and wolf behavior in general trickles down from the park biologists to the wolf watchers.

Wolf biologists in Yellowstone do not have much confidence in wolf watchers' amateur interpretations of behavior, and while wolf watchers absorb facts about behavior from biologists, it is a one-way flow of information (Smith 2019). Outside researchers in the park who had experience studying wolves in Europe and elsewhere advised me to "never believe what people say", and that what humans think howls mean in a vernacular context is unlikely to have any relation to how wolves use howling in actuality. They also lamented that visitors in YNP mostly like to hear about the life stories of individual wolves and their family drama rather than the ecology. Rick McIntyre, the recently retired ranger who accumulated over 100,000 sightings over 25 years in Yellowstone, takes advantage of this in his books and presentations. He draws in the public by recounting the lives of Yellowstone wolves like a soap opera. Both McIntyre's *The Rise of Wolf 8* and Nate Blakeslee's *American Wolf* focus on the histories of famous individuals, and many other popular books on wolves (especially the well-known wolves in Yellowstone) utilize this format when introducing a pack or attempting to impress upon readers the seriousness of losing of an important individual to interpack fighting, hunting, or poaching.

Wolf watcher communities have the potential to function as sites of vernacular knowledge production, but in Yellowstone they can appear unwilling to speculate or make conclusions based on observation that have not been corroborated by park biologists. If Yellowstone wolf watchers do not come up with new hypotheses about howling or other wolf behavior, why is that the case and does it hold true for wolf watchers in other parks and study areas? Future inquiries into this topic should include wolf watchers in different parks and compare the hypotheses and vernacular conclusions of wolf watchers with those of other groups that regularly observe wolves.

Anthropomorphism, Observation, and the Role of Folk Psychology

While some ecologists might see the soap-opera focus on individual relationships as a distraction from the real issues, it can be a useful gateway into observing the social lives of wolves and understanding the importance of individual social relationships in determining the fate of a pack. Even so, it must be handled carefully to avoid the risk of projection and anthropomorphism preventing observers from interpreting behavior in the wolves' own socioecological context.

Anthropomorphism is a buzzword and boogeyman in many books and articles, and its misuse can lead to deliberate neglect of important facets of wolf behavior. When interpreting behavior or reviewing written accounts, it is important to have a clear definition in mind in order to decide what is and is not anthropomorphic. People see anthropomorphism everywhere. Cultural and historical trends determine which traits are considered anthropomorphic (Asquith 1997). Whenever there is discussion about a feature of wolves that humans also possess, someone may come along with accusations of anthropomorphism. Even more commonly, authors attempt to defend themselves against accusations which may or may not exist.

Many writers attempt to attack or defend the use of anthropomorphism, but in the process reveal that they have not formulated a useful definition of the word and are throwing it at any instance where humans and wolves have something in common, as if it isn't to be expected that multiple social mammal species would have shared traits. Anthropomorphism is the attribution of human characteristics which the animal in question does not actually have, or the interpretation of the animal's behavior in terms of specific things a human would think in the same situation. McIntyre's presentations to the public make ample use of anthropomorphism: he

describes Yellowstone pack history in terms of how the events would be experienced by humans from a specific culture, encouraging audiences to think of their own experiences with sibling rivalry and annoying in-laws. Young and Carhart also used anthropomorphism when giving their last wolves full internal monologues. A wolf would certainly not understand the concept of a mother-in-law or wax poetic about how the reign of the wolf is over; but they do have friends, enemies, parents, and offspring which whom they share time, resources, and information.

Rick Bass, author of several short books about wildlife, consistently makes caricaturizes scientists as dry and unwilling to discuss animals' emotions. Bass does this defensively, as if what he calls his anthropomorphism (but which is usually just talking about emotions or social traits which are shared by both wolves and humans) is under attack. Off-duty scientists discuss these things willingly, while some writers—most notably Bass, but also at times Lopez, Coleman, and others—create a straw scientist to pit against themselves. This figure ignores evolutionary history and denies that any animal besides humans has the capacity to think about concepts, form social bonds, or experience emotions; the writer then gives himself the opportunity to bravely contradict the imaginary scientist. In contrast to this is Askins' memoir. Unlike Bass, Askins did not spend pages extolling her own willingness to talk about emotions and speculate about what wolves know and think. The memoir format may have provided a sense of freedom from academic expectations about limiting speculation, but Bass was also writing a popular book and yet he felt the need to defend himself whenever he mentioned a trait shared by multiple mammal species that happens to include humans.

The example of old wolves contributing knowledge and experience to their packs, something Lopez sheepishly called "anthropomorphic" in *Of Wolves and Men* (Lopez 1978, 67),

is now an accepted phenomenon in wolf biology. It would be strange indeed if a social group that uses learned skills did not benefit from the presence of more experienced group members to demonstrate hunting strategies or where to find migrating caribou. Lopez wrote about an old, toothless wolf who was well-fed but clearly not killing what she ate; but seemed confused at why this wolf was kept alive by other pack members. He offhandedly claims that "among wolves animals that don't contribute to the pack structure pass on". He does not explain what he means by 'pack structure' and seems to neglect the social nature of wolves. While many questions of apparent altruism in wolf packs can be answered by kin selection and group selection, wolves are highly emotional when it comes to social relationships and kin selection cannot explain everything. Some of the most well-known enemies observed in Yellowstone were sisters: 40F of the Druid pack and her sister 42F. 40F was considered a "tyrant" and constantly harassed her sister. In 2000, both sisters denned and the unlikable 40F received no help from any adults besides the father of her pups. Later there was an altercation that resulted in the death of 40F—the first recorded instance of an alpha wolf being killed by members of their own pack (Smith & Ferguson 2012). This is an example of how individual personalities and social drives can override what one would normally expect due to kin selection alone; and if variable social dynamics can make sisters into enemies, they can also make unrelated individuals into friends.

It is no coincidence that the traits which come up in discussions of anthropomorphism are those associated with intelligence and emotion. These are the same kinds of traits that appear in arguments about human uniqueness. Humans are only possessive over the traits they believe

make them particularly clever, altruistic, or emotional[23]. Nobody has ever accused a wolf biologist of anthropomorphism for writing about wolves' ears simply because humans also have ears. Ears are not considered an indicator of intellectual or moral superiority, so humans do not act possessive of them. Claims of anthropomorphism should be examined closely so that inappropriate attribution of human characteristics can be disentangled from humans attempting to lay exclusive claim to adaptations they share with other species.

Bekoff's (2007) discussion of "anthropomorphism" makes some important points, but also repeats the common mistake of conflating anthropomorphism with noticing similarities between humans and other species. He defined anthropomorphism correctly once, but then went on to call all sorts of things anthropomorphic when they are merely shared traits. Even after explaining that adults of many species have evolved to respond to infantile traits like large heads and eyes, he tries to claim that humans find other animals' babies cute because they look like human babies. This set of baby traits and its effects on adults are much older than humans and highly conserved, so there is no reason to call it anthropomorphism when it's human babies that look like animal babies, not the other way around. Later, Bekoff quotes primatologist Robert Sapolsky on how attributing animal characteristics to animals is not anthropomorphic, but he continues to use the word loosely.

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[23] Cultural trends determine which is most favored. Since the 16th century, Europeans have framed humans as uniquely rational, while the Japanese laid claim to being the most emotional species by focusing on the fact that only humans can laugh and cry. These trends determined the traits that humans attempted to reserve for themselves by keeping rational (in Europe) or emotional (in Japan) language out of their explanations of behavior, each considering the other anthropomorphic (Asquith 1997).

When Bekoff said humans were anthropomorphizing, he was trying to talk about a different phenomenon: the seemingly intuitive knowledge humans can have about what other animals are thinking or feeling. This is possible in part because of shared evolutionary history and physiology as well as selection pressures on accurate interpretation of another animal's motivational state.

Selection favors the ability to predict the behavior of conspecifics, especially in social group-living species like humans and wolves. There are two reasons why this ability would extend to heterospecifics. One is that some types of expressions are highly conserved across species because any changes increase the chance of being misunderstood, and the risks of misunderstanding these signals are costly. Morton's M-S rules are a perfect example: across mammals, aggressive intent is signaled by lower and noisier vocalizations which make the signaler sound larger, while friendly intent is signaled by higher and more harmonic vocalizations which make the signaler sound smaller. Changes to this pattern would be selected against because these signals allow both signalers and receivers to avoid fights, and the costs of being misinterpreted can be deadly; therefore the interpretation mechanisms that evolved for use within a species can be applied somewhat accurately to individuals of another mammal species.

The second reason is possible selection on the ability to interpret heterospecific signals and behavior. Sympatric species with common predators, including many birds and mammals, often recognize and respond to the meaning of heterospecific alarm calls (Walton & Kershenbaum 2018, Lawson et al 2020, Magrath et al 2020), and some species that interact around foraging resources like predators and scavengers feeding from the same carcass need to be able to predict the actions of their competitors. In these environments it is adaptive to be able

to interpret the emotions and intentions of heterospecifics as accurately as is necessary to predict their behavior. Whether because conserved traits make the expressive features of many mammal species interpretable by other species or because of an evolutionary benefit from understanding the intentions of certain other species, we can expect that the meaning of expressive signals are not entirely opaque to individuals outside the signaler's species.

Evidence of mirror neurons associated with determining the intentions of other individuals has been found in monkeys, humans, and rats. Mirror neurons play a part in social competence and understanding the motivational state and likely behaviors of other individuals (Kaplan & Iacoboni 2006). They are also involved in gestural communication and learning of vocal signals (Prather & Mooney 2015). If the mirror neuron system (MNS) is the basis of social cohesion across taxa, it may provide a neurological basis for humans' first impressions about the meaning of signals and expressions in other species. Mirror neuron studies have been conducted within several species (and suggested for more species that appear to exhibit emotional contagion), but not for heterospecific interactions. Experiments that would contribute to our confidence about humans' interpretations of wolves' motivations and intentions could start with domestic dogs: show human subjects pictures or video clips of dogs making happy, sad, and angry facial expressions and use an fMRI to see if the same neurons light up when humans observe these expressions in dogs as when they make the corresponding human expressions for the emotions themselves. The same could be done for vocalizations. This kind of study could be compared with conspecific studies of the same nature to see how mirror neuron activity differs in heterospecific and conspecific interactions and to what extent the MNS is important for interpreting and predicting the actions of individuals of another species.

Domestic dogs are an easy species to study because of their comfort with human environments and ability to get accustomed to laboratory settings and equipment like fMRI scanners. They are taxonomically important for understanding wolves, although they have been selected to be more humanlike, dependent on humans, and good at communicating with humans. A 2014 study asked humans to assess the emotional valence and intensity of both dog and human nonverbal vocalizations and found that they used the same features, including duration and frequency, to determine the emotional content of calls from both species (Faragó et al 2014). The humans' emotional valence ratings of dog vocalizations were fairly accurate (Andics et al 2014).

The first fMRI study comparing primates to a non-primates monitored dogs' and humans' responses to recordings of vocalizations from both species. This showed that both dogs and humans have auditory regions preferentially sensitive to conspecific vocalizations as well as a smaller portion of auditory areas that are maximally sensitive to heterospecific vocalizations (Andics et al 2014). Both species also have auditory regions that respond to emotional valence and are modulated by duration (in dogs) and frequency (in both species) according to the rules found by Faragó et al. Although both are near the primary auditory cortex, they are in different regions in the two species and display differing amounts of lateralization. Questions about homology require further comparative research, but these regions in both species respond more strongly to positive emotional valence and higher frequencies, pointing to an auditory processing explanation for call structures associated with affective content across mammals.

Askins said that "wolves and humans occupy two different cultures, and dogs act as the go-between, the translators for both our worlds." Whatever traits for social competency are shared in mammals or animals in general, or whatever has evolved multiple times in particularly

social species, the existence of domestic dogs shows that humans and wolves were already socially compatible enough to allow this domestication. Neurological studies with domestic dogs can provide information relevant to how we view the interactions of wild wolves. Humans are generally good at interpreting the meanings and motivations of domestic dogs, and it would be reasonable to expect that some of this affinity extends to wild wolves due to their shared evolutionary history, and social structures, as well as humans' history with domestic dogs.

Many humans who study wolves have heard what they call a mourning howl in contexts of grieving for a dead packmate. In concordance with Faragó and Andics' findings on how humans and dogs interpret duration and frequency with respect to emotional valence, mourning howls have been described as particularly long and low compared to other howls. The mourning howl has not been described in a peer-reviewed paper, but it consistently appears in books and non-peer reviewed articles by everyone from anthropomorphic writers to wolf researchers who have learned to recognize it after observations of death in wolf packs.

John and Mary Theberge described how an Algonquin wolf was shot after following deer out of the park in February of 1991; later they heard one of the pack members repeating "long, forlorn notes breaking downward in melancholy intervals". They said "from past experiences we recognized the howl as one we had come to call the 'mourning howl'. We have heard it both in the wild and in captivity when a packmate has been injured or killed" (Theberge & Theberge 1998). While they may describe this kind of howl and its presumed emotional referent in a scientific context (as an observation waiting to be quantitatively verified), it is unlikely that the Theberges or anyone else would have used "forlorn" or "melancholy" in the howl description if they hadn't been writing for a popular audience.

Steinhart (1995, 90) quoted Jason Badridze, who attempted a cultural-immersion type study on Georgian wolves in the 1970's and claimed to recognize a howl for loneliness: "it must be a universal language". While there are neurological structures that tend to lead humans in the right direction when it comes to judging the affective content of mammal vocalizations, they could also lead to some of the most common misinterpretations. All wolf howls are long and low compared to human speech, but if we have evolved to equate these acoustic properties with sadness, we could easily misinterpret any howl as sad or lonely. Humans who are accustomed to hearing wolf howls in context might not make this mistake (Steinhart emphasizes the importance of experienced observers) and researchers who talk about the mourning howl describe its acoustic properties in contrast to other kinds of howl; but we also know that humans' biases and expectations can seriously distort how they hear and interpret vocalizations. Humans in situations where they can observe mourning howls are always familiar with the pack and thus may experience grief or stress at the same time as the surviving wolves are vocalizing. Aside from expectations, some hormones can affect hearing by increasing the excitability of auditory neurons and increasing sound discrimination and memory in songbirds and mammals (Tremere et al 2009, Bark et al 2009), and grief-related chemicals in the brains of human observers might be able to influence how they hear the howls in context.

Experiments are needed to confirm the existence of mourning howls and the ability of humans to distinguish them. Howls recorded after the death of a pack member and howls recorded in another context should be put through a PCA and DFA, similar to the individual ID studies and Watson's context study, to see if they are discriminable. Humans who claim to be able to recognize mourning howls should be placed in an experiment where they listen to

recordings of howls from mourning and non-mourning contexts and try to identify the mourning howls without any context clues. Studies of objective acoustic structure, research on perception and neurology in humans and domestic dogs, and both wild and captive ethological studies of wolves' responses to vocalizations and their use of howls in the wild are necessary. All of these studies can contribute to making educated decisions about how to interpret historical and vernacular howl descriptions.

These descriptions must be approached with an eye to the ways knowledge is created outside of institutional structures. In the 1810's, before the professionalization of many scientific fields, all of American science was vernacular in nature; small experiments and individual observations were spread through networks of correspondence until they formed knowledge or consensus (Valencius 2013). Even earlier, fact-making in natural history was done through extensive observations forming a pool of knowledge. In contemporary biology, these methods are seen as a background for institutional science. Slobodchikoff and Bekoff both emphasize the importance of extensive observation and how the collection of anecdotes can form a knowledge base from which to harvest hypotheses and make informed decisions about study design.

Darwin and Romanes made use of collected anecdotes from scientists and popular accounts to describe the continuity of animal expressions (Asquith 1997), but later experimental behaviorism turned psychologists away from anecdotes. In the 1990's, anecdotes were considered suspect but sometimes admissible as a starting point. Gould & Gould (1994, 160) related some incidental observations of deception among chimpanzees and then qualified them: "Of course such reports are anecdotes, but the behavior in question was observed by experienced

researchers. Because of its novelty, each inventive ploy is by its nature a unique event." Anecdotes counted as relevant observations, but only when the observer was an experienced scientist. Observations of rare or unique behaviors by amateur wildlife watchers would have been inadmissible because the observer's lack of expertise was assumed to indicate a judgment clouded by cultural biases.

Conevery Bolton Valencius (2013) studied the production of vernacular knowledge about earthquakes and the forgetting of that knowledge after seismology became a professional field that only accepted certain kinds of data and methods. The same may have happened to indigenous knowledge about wolf communication in North America, with information being lost under the dual effects of scientific professionalization and colonialism.

An example of a site of indigenous knowledge gained through accumulated observation and experience is the network of Nunamiut hunters in Alaska. In the 1970's, Robert Stephenson apprenticed with semi-nomadic hunters in the Nunamiut village of Anaktuvuk Pass in the foothills of the Brooks Range (Fritts et al 2003). The Nunamiut, who had lived in the Brooks Range area for several generations as of 1949, maintained the same lifestyle for centuries with the addition of guns; although increasing access to modern transportation beginning around 1950 eliminated the need for seasonal migrations for trade. While they primarily ate caribou and other game animals, they also hunted predators including wolves for their pelts; and by the 1940's, occasional rabies outbreaks caused some wolves to get too close to camps and attack humans and dogs. Despite the occasional danger from a rabid wolf (a phenomenon which caused Europeans to fear all wolves as potentially vicious) and the regular use of wolves as an economic resource, wolves were still respected in the Brooks Range region, especially for their skill as hunters.

When Stephenson traveled with Bob Ahgook, Justus Mekiana, and other experienced hunters, he aimed to learn what they knew of the "parts of [wolf] life that had not yet made it into professional journals". Barry Lopez, author of Of Wolves and Men (1978), went to the Brooks Range with Stephenson and the hunters in the late 1970's and saw that Stephenson had learned things from traveling with the hunters that professional biologists knew nothing about, such as how wolves identify which of two valleys is likely to provide the most prey and how to sex and age a wolf at long distances (Lopez 2020). The Nunamiut in Anuktuvuk Pass impressed Stephenson with their knowledge of wolves derived from consistent interaction with the wolves and their environment in open terrain which provided ample opportunities for observing the wolves' natural history and individual differences. Knowledge of individual temperaments and the ability to sex and age wolves from a distance allowed for more accurate interpretation of events and the ability to predict behavior. The conceptual picture of wolves in this region was more specific than the generalized wolf found in discussions by 1970's biologists: the Nunamiut almost never talked about wolves as a monolith, but talked about certain wolves (with respect to individual differences in morphology and temperament) and wolves under certain environmental conditions. Contemporary studies of wolves and other intelligent, flexible animals should approach behavior in a similar way, tracing behavioral diversity to its sources in terms of individual temperaments, individual experiences (including learning and memory), group dynamics, and ecology.

The tendency to overgeneralize likely stemmed from methods developed for studying species with less flexible behavior. While the humans in this region were directly competing with wolves for prey and hunting them for their pelts, there was no animosity and none of the

"hate, rancor, or guilt" commonly associated with wolf-killing by Europeans and Euro-Americans; they also lacked the irrational fear of non-rabid wolves exhibited in settlers' campfire stories. Stephenson wrote that "the intelligent and social nature of the wolf is cause for real admiration among the Nunamiut", and that when asked about wolves, the Nunamiut always emphasized their intelligence. Stephenson discussed intelligence in the context of hunting and foraging such as learning how to hunt in different conditions, how to set up an ambush, which carcasses to avoid (wolves who have escaped from traps are suspicious of any carcass that human have tampered with and don't let their pups go near them), and strategies that take advantage of snow depth and landscape features (Stephenson & Ahgook 1975). While the Nunamiut hunters deduced the locations of den sites from hunting wolves' movement patterns, their experiences at the dens were restricted to acting as predators and observing defensive responses from different adults, so their primary source of observation on relaxed social behavior was probably the play of older pups, yearlings, and adults in the open.

Stephenson and Ahgook wrote that Nunamiut hunters called wolves into rifle range "by imitating certain wolf howls", implying that the hunters were aware of at least some disparate howl types and enough about meanings to know which howls were most likely to elicit approach. Professional biologists around that time were using howl playbacks and imitated howls to assess wolf responses in the wild (including vocal responses and approaches), but if they are unaware of the meaning of their stimulus howls, some of the apparent differences in approach rates between different populations could be an artefact of using howl stimuli with different meanings.

Stephenson concluded that observation is not only a source of knowledge but also the key factor determining humans' opinion of wolves. He linked biases about wolves to whether the

humans in question live in an open or forested habitat. Peter Steinhart also discussed how cultural perceptions of wolves can change with differences in visibility. When humans can see wolves in the wild on the open tundra or plains, they share stories about them and learn about their behavior from observation. Humans in forested areas don't often see wolves but they do see their kills, which leads them to fear the wolves as predators (Steinhart 1995, 332-337). Watching wild wolves in the open tundra or in places like Yellowstone with high visibility, one quickly learns not only that hunting is more difficult than one imagines but that a large portion of wolf life consists of sitting around with packmates, napping, and playing. Impressions of wolves in tundra and plains cultures are shaped in part by the ability to see wolves as social animals:

> When people study and reflect on the life of the Wolf, they can see that his ways are similar to those of human beings. Family seems to be important to the Wolf, and he not only feeds and protects his own and the pack, but he nurtures and cares for them as well. Perhaps, like the Lakota, he tells his children and grandchildren the ways of the grandfathers who have gone before, ways that would enable them to live in harmony not only with their own kind but with other nations as well. For it is within the confines of the family that the ways of life are passed on, and in doing the nation not only survives, but is made stronger (Manuel Iron Cloud cited in McIntyre 1995, 261).

These things imply that long-term basic ethological observation in and outside of professional scientific structures may not only lead to the creation of knowledge and an informed base for future research but also ameliorate some of the effects of cultural biases in the observers.

Sigurd Olson said his conclusions came from "many years of experience in the north, unfortunately not always from carefully kept notebooks". After traveling the region and observing wolves and their environment from 1920 to 1938, he came to general conclusions which he was confident enough to include in his paper. He acknowledged fact-building outside of scientific references, as he came to many of his conclusions through experience and time spent

in the field: “like those of most other woodsmen, they are the sum total of experiences and general working knowledge for which it is impossible to cite authority accurately” (Olson 1938).

Many professional scientists assume that their work is inherently the most objective and that their knowledge is the least polluted by cultural biases or anecdotal evidence. In wildlife biology, especially when it comes to behavior and interactions, the most important research method is consistent observation of the same animals in the same places over long periods of time. While biologists are faced with short-term grants and pressure to be efficient, amateur observers such as hunters who spend a lot of time learning the land and observing wolves on their level can develop a more complete knowledge about the aspects of wolves that are relevant to them. Biologists like Haber who are not stretched thin between different projects and are able to devote more time to basic observations in the wild collect the same kinds of information. Wolf biologists in more standard studies including Doug Smith and Dave Mech have also said that they know more about wolves from field experience than they have ever published in journals.

It seems that humans are capable of interpreting the communication of wolves to some extent outside of a scientific paradigm, but just like within ethological research, it requires long hours of observation and intimate knowledge of the land and the context of possible referents. The boundary between amateur wolf watching and conducting a long-term observational study like Haber’s is porous, and even humans who spend a lot of time in wolf habitat can be misled by their own biases; a human who is afraid of wolves will always imagine danger upon hearing a howl, regardless of the meaning of the howl and how much experience the human has.

Nonetheless, for all the reasons explored in this chapter, it is not an entirely futile effort to look for information about wolf communication in vernacular descriptions of their howls and

behavior. Although many historical accounts portray the author's biases so strongly that it seems as if nothing else can be taken from the record, their intuitive responses to vocalizations must have ultimately been driven by vocalization-sensitive neurological structures that evolved to respond to auditory features associated with affective content. Underneath layers of cultural bias lies shared evolutionary history of which ethologists should not be afraid to take advantage.

Some anthropomorphism or projection is inevitable when trying to interpret the intentions of another organism, even a conspecific. As Romanes said, one's own mind is the only available model for subjectively understanding how others think. It can never be completely accurate, but it is based on evolutionary continuity and a history of selection pressures favoring social competency. Vernacular descriptions and compilations of anecdotes reveal folk-psychological explanations that may be more accurate than one would assume if they were driven by culture alone. Instead of avoiding folk psychology and assuming one mammal's intuition about another mammal's motivational state must be incorrect, we can take advantage of our shared evolutionary history. Amateur explanations, indigenous knowledge built on generations of observation, and the intuitive impressions of researchers in the field can be taken as starting hypotheses for the further study of the meaning of wolf howls and other animal communication. Continued research on the anatomy, evolutionary history, and accuracy of humans' intuitive interpretations of emotional content in animal vocalizations should remind behaviorists that referring to shared traits is not anthropomorphic. Historians and biologists alike should locate past and present sites of vernacular science and put in their own time observing wolves in the wild.

CHAPTER FIVE

WOLF HOWLS AND CONTEXT IN YELLOWSTONE NATIONAL PARK

The general functions of wolf howls are well studied, but only a few papers deal with questions about semantic meaning available in the structure of a howl rather than its context. This is a question of interest for gleaning behavioral and contextual information in the field when wolves are audible but not visible, and for understanding more about the social and cognitive aspects of wolf communication. Wolf howls, being the primary long-distance communication method of a cooperative predator, should also be on the radar for those interested in the evolutionary context of human communication.

In 2016-17, I collected and processed data for a wolf howl project run by Sara Waller and Arik Kershenbaum, members of the Cooperative Predator Vocalization Consortium (CPVC). Their project required wolf howls recorded by passive monitoring equipment along with their times and locations, but the data did not include observation of behavioral contexts. Investigators and technicians were not present while most of the howls were being recorded, and more howling events were recorded than those that occurred in daylight while the howlers were visible from the road. I used the CPVC data from the 2016-17 season to investigate the benefits and drawbacks of some current methods in wolf howl research.

Here I will explain my attempt at using howler location as a proxy variable to discern territorial and non-territorial messages in howls recorded from wild wolves, including some meta-analysis of the acoustic variables found to be important in different howl categories in earlier papers, where they agree and disagree, and what it implies for current methods of describing continuous vocalizations. I will ultimately argue that while passive monitoring is

beneficial for some types of research, studies on possible content and meaning are not viable without concurrent observation of behavioral contexts.

Study Area

The northern range of Yellowstone is a highly contested area for due to the abundance of prey. The largest elk herd in the Yellowstone ecosystem winters there because it offers lower snow depth than the interior and better access to vegetation. The park interior has fewer elk, and interior packs have to hunt more difficult prey (bison and sometimes moose) during winter by forcing them away from thermal features into the deep snow where wolves have an advantage.

Only one pack, the Mollies, lives entirely on bison in the winter. As of 2012, the Delta pack (disappeared in 2015) was the only one that would eat moose (Smith & Ferguson 2012). Moose are difficult prey; the wolves in Denali learn to hunt moose through cultural transmission of strategies developed by packs that have spent several generations in the same territory with the same prey base (one example is a nose-grab strategy, where at least one wolf grabs the moose's nose or otherwise distracts the large animal's front end while the others come from behind to make the kill). There have now been approximately 6 generations in Yellowstone since the reintroduction (generation time of 4.16 years calculated by Vonholdt et al 2008), and packs in the interior may have more continuity and fewer disruptions than those on the northern range, although Mollie's wolves do range out of the park on the south side. The longest-lived pack in the park is Crystal Creek/Mollie's at 25 years (Smith et al 2020).

There are fewer thermal features in the north, but more grass at the lower elevations encourage elk to winter in the Northern Range, which is why 50% of wolves live in 15% of the park, mostly concentrated in the north (Smith & Ferguson 2012). The northern range averages

52.9 wolves/1000 km^2, almost double the density of Minnesota and 10 times the density of Denali National Park (Cassidy et al 2016). Increased density leads to more competition and higher risks of conflict and skirmishes along territory borders (Smith & Ferguson 2012).

Background on Howls

Selection should favor frequencies that can carry a signal as far as necessary, not as far as possible. Some signals would be disadvantageous to transmit too far, depending on the information available in the signal and who else may be present in the environment and able to intercept a signal to the signaler's disadvantage (Richards & Wiley 1980). Especially in territorial species, signals can include components (like higher and lower frequency bands) that degrade predictably so that the distance can be assessed by comparison of the attenuation of different parts of the signal (Naguib & Wiley 2001).

Acoustic signals that that need to maximize distance and minimize distortion generally use harmonically purer sounds (Harrington & Asa 2003); howling fits the general pattern for long-distance vocalizations (low pitched and harmonically simple), so it is usually reasonable to ignore sounds that are not harmonics and assume non-harmonics in the recordings are noise. Fitting a howl to a function consisting of Lorentzian peaks at exact multiples of each other (Root-Gutteridge et al 2013) ensures that only true harmonic sounds are included. The same assumptions could potentially be used to pull a single howl out of a chorus because the fundamental frequencies of howls joining after the initial howl usually differ by at least 15 Hz (Harrington & Asa 2003), although a given wolf may vary the frequency of their howls within a bout depending on motivational state, social context, and changes in the acoustic environment including other howling pack members. However, howls can include noisy segments, and their

features may be relevant to howl meaning. Some territorial howls contain non-harmonic components, and Harrington (1987) observed that wolves who closely approached a human howler were more likely to include noisy sidebands at the end of their howls. Harrington's study showed that when responding to human howls, wolves who were willing to approach a potential intruder used lower and harsher (noisier) howls, as predicted by Morton's M-S rules. Because the context of these howls was close approach, these territorial response howls may not have been constrained by the same requirements of territorial advertisement howls which must be heard from longer distances. Aside from being associated with large body size and aggression, noisy components also make the howls easier to locate, which may allow receivers a chance to avoid a dangerous confrontation. Whatever the case, this does show that non-harmonic sounds cannot always be ignored in the study of wolf howls.

Information is encoded in modulation (variations in frequency or amplitude over time) (Richards & Wiley 1980), so the amount of information in a signal is limited by the range of frequencies and amplitudes available. Higher frequencies drop out of a signal sooner than low frequencies as they are attenuated more quickly; low frequencies are better for detection over long distances (Smith 1977). Amplitude fluctuations in a sound arise primarily from scattering (air turbulence) and increase with distance and carrier frequency; at long distances, random fluctuations could exceed amplitude modulation in a signal (Richards & Wiley 1980). Lower frequencies and repeated, stereotyped modulation patterns are best for detection and discrimination of long-distance auditory signals; the inclusion of features that degrade predictably with distance (such as higher and lower frequencies) increases locatability (Wiley & Richards 1978). A long-distance vocalization like a howl should rely primarily on frequency

modulations within low to intermediate frequencies. The 1-4 kHz range is best for minimizing attenuation near the ground, and the 2-7 kHz range is best for minimizing reverberations (Richards & Wiley 1980). Frequency modulation is important for long-range acoustic signals because reverberation and intensity fluctuation primarily affect the amplitude patterning of a signal. Frequency modulation allows for greater power per Hz bandwidth and increases the signal to noise ratio. When amplitude modulation is used to encode information at long distances, it requires redundancy to avoid signal degradation (Richards & Wiley 1978).

Methods and Results

Collection

Howls were recorded by four SM3 recording units placed on the northern range of Yellowstone National Park in and around the Lamar Valley from November 2016 to April 2017 under permit number YELL-2017-SCI-6062. The units were placed in inconspicuous locations within 1.3 km of each other and at least 1 mi (1.6 km) away from known wolf or carcass locations. Units recorded continuously while battery life allowed, and batteries were replaced twice a week during the season. The SM3 GPS provided location data and accurate time synchronization using a GPS clock. The units were moved three times over the course of the season to locations selected based on information on recent pack sightings from park ranger Rick McIntyre and wolf watcher Ilona Popper. As the winter season is when wolves travel frequently and do not stay at predictable homesites as they do in summer while rearing pups, pack movements were unpredictable and howl recordings were opportunistic and did not deliberately target certain packs.

Howling events were identified by visual inspection of the spectrograms in Raven Pro and then individual howls were selected for analysis based on recording quality and absence of noise. Chorus howls were excluded from the dataset because of the difficulty of isolating single howls from a chorus.

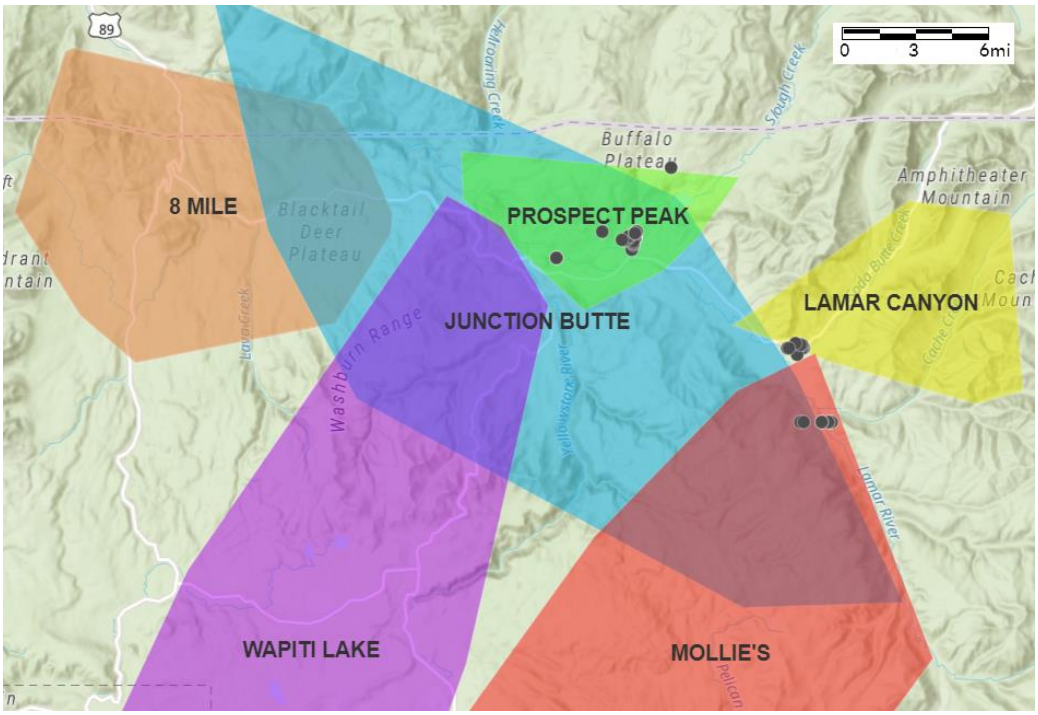

Figure 1. Located howls with respect to territory MCPs from 2017.

Localization

Howls were localized by triangulation using a Matlab script from Arik Kershenbaum. This method can determine the location of a vocalizing animal at distances of up to 7 km within an error of ~20 m (Kershenbaum et al 2019). Howls that could not be triangulated because they were not picked up on at least three recorders were dropped from the data, as were howls for which the recorder lost the GPS signal and therefore could not provide accurate timestamps. Latitude and longitude were calculated for each howl that had sufficient data. These locations were then checked against collar data from the Yellowstone Wolf Project (National Park

Service) containing known locations of collared wolves within 1.3 km of the recording units during the study season. Unlike the wolves in Poland who only howled from the centers of their territories year-round (Nowak et al 2007), the wolves on these winter recordings howled both in territory interiors and near the edges and borders of overlapping territories.

November 2016, December 2016, and April 2017 were excluded from localization because the necessary metadata files were missing from the recordings made during these months. This prevented a comparison between howls in the seasonal contexts of spring (breeding) and fall (leaving homesites). The final dataset was comprised of howls from January, February, and March of 2017.

Isolation

Howls were isolated from background noise using GeneralHowlTracer, a Matlab application made by Kershenbaum. This program displays each howl as a spectrogram and allows the user to click along the fundamental frequency contour. The rest of the fundamental is filled in 0.02-second timesteps.

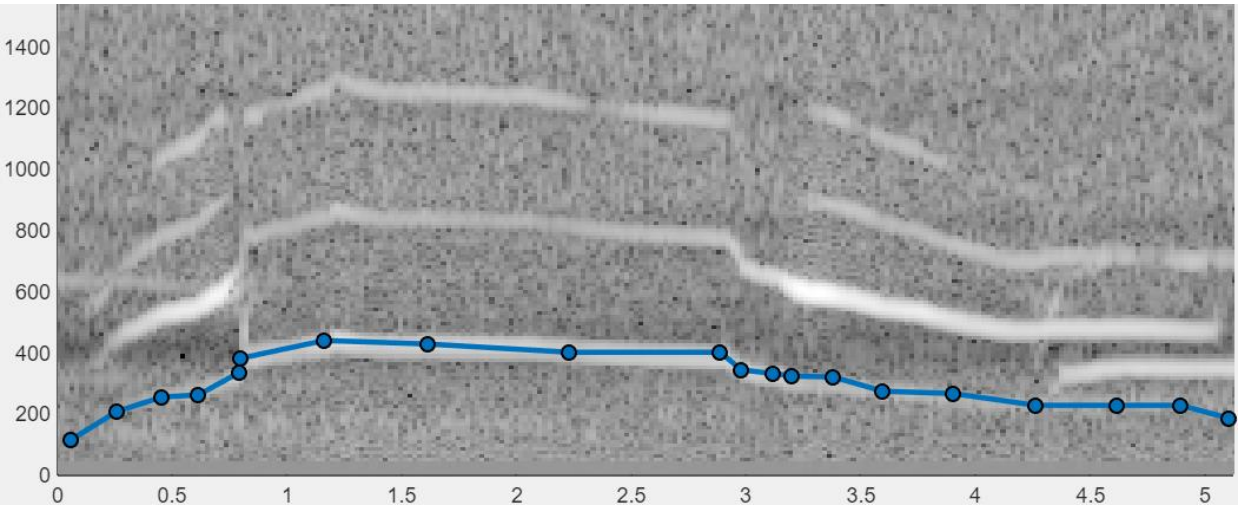

Figure 2. GeneralHowlTracer uses input points to determine the fundamental frequency contour. In this example, another howl beginning in the last second of the target howl is easily excluded.

Howl Parameters (response variables)

The vast majority of wolf howl papers dealing with acoustic structure are either concerned with describing the overall structure of howls from different species, subspecies, and populations or with determining which features vary with individual ID. Papers on individual ID do not all agree on which variables are statistically significant for individual discrimination. Only one paper has examined howl features with respect to contexts.

Some potentially informative variables were left out of this analysis due to the constraints of recording in the wild with variable distances from the recorder to the vocalizer and various weather and geography conditions that could have affected attenuation. Palacios et al (2007) and Tooze et al (1990) found the maximum number of harmonics to be significant in individual ID, but as the upper harmonics in wolf howls attenuate very quickly over distance (Harrington & Asa 2003) and over long distances from recorders in the wild many of the higher harmonics attenuate fully before reaching the microphones, I omitted both this variable and normalized amplitude variables significant in the analysis of Root-Gutteridge (2013) that have to do with harmonics. I consulted with Root-Gutteridge and Kershenbaum on howl extraction and variables, and they confirmed that the quality of recordings in Yellowstone was not sufficient to allow the inclusion of amplitude and energy variables because of the noisy conditions and long distances from recorders. Amplitude variables have been used to improve individual ID in recordings of some wild wolves (Root-Gutteridge et al 2014b), but those were higher-quality recordings compiled from sound libraries. Future research on this topic will require more deliberate setup of recorders to obtain howls from the wild with usable amplitude variables. Root-Gutteridge believes wolves may use amplitude modulation to emphasize parts of howls the way humans emphasize words and syllables, so future research may reveal that amplitude modulation is

relevant to a howl's message or to relative emphasis on different messages (e.g. the amount of urgency associated with a message in a section of a howl or howling bout). For the same reasons, I was also forced to exclude some variables that were significant in howl context in what is currently the only paper of this kind on the relationship between howl structure and context (Watson et al 2018). These include time at max intensity (percent of the howl for which intensity was at maximum), FPeak (the frequency with the highest energy), and EFPeak (the energy of the FPeak or maximum energy).

I included duration of noisy bands in the howls, measured before the isolation protocol and expressed as a percentage of the howl's duration. Most howl analyses exclude non-harmonic sounds because harmonic tones are the parts of howls that can carry the farthest distances, but some territorial howls do use non-harmonic components (Harrington 1987). The length of non-harmonic sidebands may be relevant to individual ID (Tooze et al 1990)[24] as well as territorial messaging. Nonlinear features of mammal vocalizations have communicative potential (Wilden et al 1998), and it is possible that there are semantic properties of noisy bands in howls beyond their presence and length.

The amount of frequency modulation in a howl is usually expressed in terms of the number of inflections (changes in sign/direction), frequency range, number of discontinuities (arbitrarily defined as changes of more than 25 Hz in one timestep), coefficient of frequency

[24] It could be that noisy bands are simply an affective expression that indicates competition or territoriality, and the individual differences found by Tooze et al (1990) were due to personality or rank differences (some of the captive wolves in the individual ID experiment were more competitive or territorial).

variation (ratio of the standard deviation to the mean), and the coefficient of frequency modulation (CoFM= $\Sigma \frac{|f(t)-f(t+1)|}{n-1} * \frac{100}{\text{Mean}F_0}$). CoFM is not a standard statistic in bioacoustics (Root-Gutteridge, personal communication), but has been used in wolf howl papers since the late 1980's. Because it is unclear why a measure of differences should be normalized by the mean frequency[25], I replaced CoFM with the average difference in fundamental frequency between consecutive time steps (MeanDiff= $\Sigma \frac{|f(t)-f(t+1)|}{n-1}$).

Table 1. Howl parameters used and significance in earlier studies.

PARAMETER	DEFINITION	SIGNIFICANT IN
Duration	t(start)-t(end) of fundamental	Context (Watson et al 2018) Pack ID (Zaccaroni et al 2012)
Mean F_0	Average of F_0 across howl	Individual ID (Root-Gutteridge et al 2014, Palacios et al 2007, Tooze et al 1990) Individual discrimination (Palacios et al 2015) Pack ID (Zaccaroni et al 2012)
Mode F_0	Most common frequency	Pack ID (Zaccaroni et al 2012)
Start F_0	F_0 at start	Context (Watson et al 2018)
End F_0	F_0 at end	Context and individual ID (Watson et al 2018) Pack ID (Zaccaroni et al 2012)
Max F_0	Maximum F_0	Context (Watson et al 2018) Individual ID (Palacios et al 2007, Tooze et al 1990) Pack ID (Zaccaroni et al 2012)

[25] The way wolf papers have calculated CoFM since Harrington (1989) and Tooze (1990) began using it, a howl with the frequencies [220, 280, 310, 290] would have a lower CoFM than a howl with the frequencies [120, 180, 210, 190] because its mean frequency is 100 Hz higher, even though the differences [60, 20, 10] are the same. This statistic appears in Harrington and Tooze as well as Palacios et al (2007), Passilongo et al (2010), Zaccaroni et al (2012), and Root-Gutteridge et al (2014a); a different variant appears in a paper on dingo howls (Deaux et al 2016) which divides by 100 instead of multiplying, but it still divides by the mean and creates a false indication of less frequency modulation in howls with higher mean frequencies.

Min F_0	Minimum F_0	Context (Watson et al 2018) Individual ID (Tooze et al 1990) Pack ID (Zaccaroni et al 2012)
Posmin	Position of Max F_0 = time of first Max F_0 as a percentage of the duration	Individual ID (extracted howls; Root-Gutteridge et al 2014)
Posmax	Position of Min F_0 = time of first Min F_0 as a percentage of the duration	Individual ID (extracted howls; Root-Gutteridge et al 2014)
Range F_0	Max F_0 - Min F_0 in (Hz)	Individual ID (Tooze et al 1990) Pack ID (Zaccaroni et al 2012)
Time Max F_0	Percent of duration for which F_0 is at a maximum	Context (Watson et al 2018)
MeanDiff	Average difference in frequency between consecutive timesteps of the fundamental = $\Sigma \frac{\lvert f(t)-f(t+1)\rvert}{n-1}$	*replaces CoFM, which was significant in:* Individual ID (Palacios et al 2007, Tooze et al 1990) Pack ID (Zaccaroni et al 2012)
CofV	Coefficient of frequency variation = (SD/MeanF_0)*100	Individual ID (Root-Gutteridge et al 2014, Tooze et al 1990) Pack ID (Zaccaroni et al 2012)
Abrupt	Number of discontinuities (changes of >25Hz in one 0.02 s timestep) in the fundamental	Individual ID (Tooze et al 1990) Pack ID (Zaccaroni et al 2012)
Change F_0	Number of inflections in the fundamental	Marginally important in individual ID (Tooze et al 1990)
Noisy Band	Duration of non-harmonically related frequency sidebands	Marginally important in individual ID (Tooze et al 1990)
Noisy band location	Start, middle, end	Noisy bands at the end were more territorial (Harrington 1987)

The most common method of describing a wolf howl is by taking small timesteps of the fundamental frequency contour and using a variety of variables intended to capture information about the shape. However, much of the howl shape is not captured by these kinds of variables. The set of variables used by most howl papers would not be able to distinguish between a howl and the same howl played backwards, which means they are missing aspects of the howl shape

that are relevant to a wolf's perception. There are variables meant to capture the amount of frequency or amplitude modulation across the entire howl (MeanDiff, Abrupt, ChangF, etc.), but the papers that attempt to describe where things take place within a howl do it very broadly (such as isolating the slope of the first rise, including the positions of howl maxima and minima, or the locations of local maxima). If there is any semantic information contained in something like the specific sequence of slope changes in a howl's structure, current methods of howl analysis would not be able to detect it. Future studies comparing howls from different individuals, groups, or contexts may benefit from following Kershenbaum et al (2016) in using a dissimilarity matrix and clustering algorithm to see if howls from the same individual, group, or context are more similar to each other than they are to other howls in the dataset—although this kind of method would not result in a list of acoustic features that correlate with a context or message.

Another issue with the common method is that papers largely disagree on which variables are important. Four papers looked at individual ID: Tooze et al 1990, Palacios et al 2007, Root-Gutteridge et al 2014, and Watson et al 2018. All tested discrimination using a DFA. Two used PCA to reduce the set of variables before the DFA. This should not have had an effect on which acoustic parameters turned out to be important for discrimination. If the Mean F_0 is important for individual ID information in howls[26], it should be important in the discriminant function in papers that only used DFA, and it should correlate with important PCs in the papers that used a

[26] Mean F_0 was significant in every study of individual ID except Watson's. This is likely due to small sample size, as mean F_0 is important for individual ID across mammal vocalizations.

PCA and a DFA. Every paper that asked about individual ID has found that howls from different individual are discriminable, but they don't agree on the significant parameters. Table 2 demonstrates the disagreements between individual ID papers; every variable that was important for individual ID in at least one paper's DFA is included.

Table 2. Disagreements in what variables contribute to individual ID information in howls.

Individual ID variables	Tooze et al 1990		Palacios et al 2007		Root-Gutteridge et al 2014		Watson et al 2018	
	included	significant	included	significant	included	significant	included	significant
Mean F_0	✓	✓	✓	✓	✓	✓	✓	
End F_0	✓		✓		✓		✓	✓
Min F_0	✓	✓	✓		✓		✓	
Max F_0	✓	✓	✓	✓	✓		✓	
Duration	✓	✓	✓		✓		✓	
Range F_0	✓	✓	✓		✓			
Posmax	✓		✓		✓			
CofM	✓	✓	✓	✓	✓			
CofV	✓	✓	✓		✓	✓		
Abrupt	✓	✓	✓		✓			
Changf	✓	✓	✓					
MaxHarm	✓	✓	✓	✓				
Dside	✓	✓						
Q25%							✓	✓
NorAmp2 Mean					✓	✓		
NorAmp3 Max					✓	✓		

Howl Classifications (explanatory variables)

Borders. Howling near borders may be particularly important in preventing trespassing, maintaining interpack spacing, and avoiding agonistic encounters. In the 1970's, researchers estimated the location and width of buffer zones or contested regions between territories as approximately 2-km-wide strips (1 km to either side of a territory edge) based on the higher

density of surviving whitetail deer, implying that wolves spend less time in those areas. The existence of buffer zones with an increased risk of intraspecific conflict was not proven until a large enough sample was collected, which required over 20 years of radiocollar data (Mech 1994). From 1968-1992 in Superior National Forest, 91% of wolves killed by other wolves were within 3.2 km of a territory edge and 41% were within 1 km, in the Yukon 35% were killed within 2.5 km of an edge, and in Denali 75% were killed within 3.2 km of an edge (Mech & Boitani 2003). Three border variables (1 km, 2 km, and 3 km) were examined for the Northern Range howls. The howl locations were mapped onto pack territories in ArcGIS Online using minimum convex polygons (MCPs) from the Yellowstone Wolf Project for 2017 and each howl was assigned a 1 or 0 for each border variable based on whether they fell inside buffers of 1, 2, and 3 km on either side of an MCP border. The 3 km buffer was thrown out of this analysis because only 6 of 77 howls did not fall within 3 km of at least one border. The northern range of Yellowstone contains several overlapping territories such that one pack's border can pass through another pack's interior. Small territories are also viable in this region because of the high prey density, so packs like Lamar Canyon and Prospect Peak have very little interior territory that is more than 3 km from their borders. In a cluster of howls near the middle of Prospect Peak territory, most fell within 3 km of the border.

Here, the buffer zone is used as a proxy for territorial messaging. The implicit assumption is that howling near the border is territorial and directed at other packs and extra-pack wolves, while howling in the interior of a territory is directed at packmates and has to do with things like social cohesion or locating each other rather than territorial advertisement. This assumption should be considered tentative and subjected to further investigation. Wolves do howl for

territorial reasons from the inside of their territories, especially if they are defending an important resource such as a carcass or a rendezvous site with pups (Harrington & Mech 1978). Wolves can hear howls from at least 10 km away in forested areas with favorable weather conditions, and humans can hear wolves from 16 km away in open tundra (Harrington & Mech 1978), so a pack would not need to approach the buffer zone to send a territorial message to a neighboring pack. However, if wolves are already near the border, they may be more concerned with territorial advertisement and motivated to howl because of preexisting knowledge of the neighboring pack's territory or detection of scent marks in their vicinity. Interpack howling sessions are most likely when packs are near a common border (Harrington & Mech 1978).

Harrington and Mech (1978) pointed out that responding to strange howls is useful for preventing accidental encounters with other packs, but staying silent is more useful for preventing "deliberate encounters" or attacks which could be mounted by a resident pack against an intruder or even by intruders against residents. Accidental encounters with non-packmates are most probable near territorial borders and "would be most common in the roughly 2 km of territory overlap between adjacent packs" (Peters & Mech 1975), so there may be more pressure in favor of spontaneous howling and responding to howls in and around the buffer zone. Wolves near a border could also howl for non-territorial reasons; they may howl to locate their packmates while hunting or patrolling, or howl in response to packmates howling from the inside of their territory. Wolves who are alone or in small groups should be under more pressure to avoid deliberate encounters, and as expected smaller groups respond to human howls at lower rates (Harrington and Mech 1978).

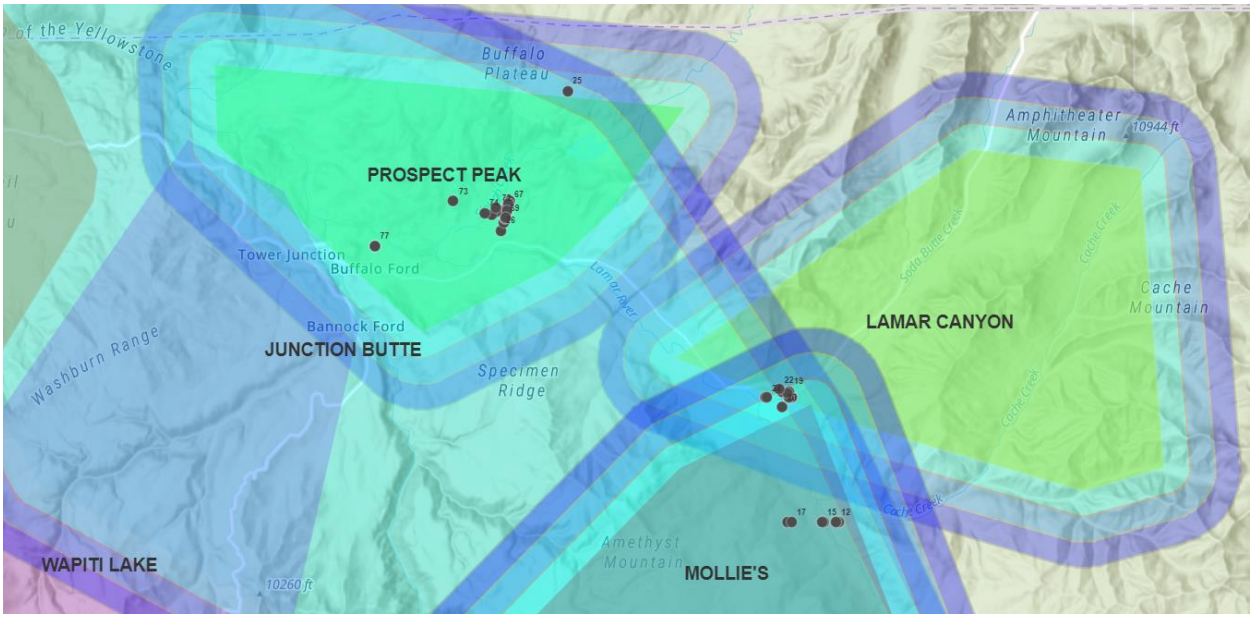

Figure 3. Localized howls with 1, 2, and 3 km buffers around the territory MCPs. Only outer buffers are shown here, but howls were classified as inside one or more of the border variables if they fell within 1, 2, or 3 km on either side of the border.

Packs. The dataset consisted of 9 known Lamar Canyon howls and 47 known Prospect Peak howls; the rest were not identifiable from their locations and sighting reports. Pack or group signatures are unlikely to be detected in this context, and each pack's howls could contain a lot of pseudoreplication because of the same individuals, likely the alpha paid, being overrepresented in the howling compared to other pack members.

Month. All the locatable howls were around breeding season, but February is the prime breeding month. If February howls are differently structured from April and March howls, it may have to do with a breeding-related messages or motivational states.

Pre-Chorus. 20 of the howls were leading up to a chorus and 57 were not. If howls that initiate a chorus group together, it could point toward acoustic features of intrapack messages. However, this question should be examined with more packs, as any grouping in this dataset is likely to be because of the same individuals (mostly alphas) initiating most of the choruses.

Results

Principal component analysis was used to reduce the set of 17 acoustic measurements to a small set of uncorrelated variables. While some analyses only use a DFA (Palacios et al 2007), others reduce the variables using PCA to get rid of extraneous variables and contribute to more accurate discrimination (Watson et al 2018, Root-Gutteridge et al 2013).

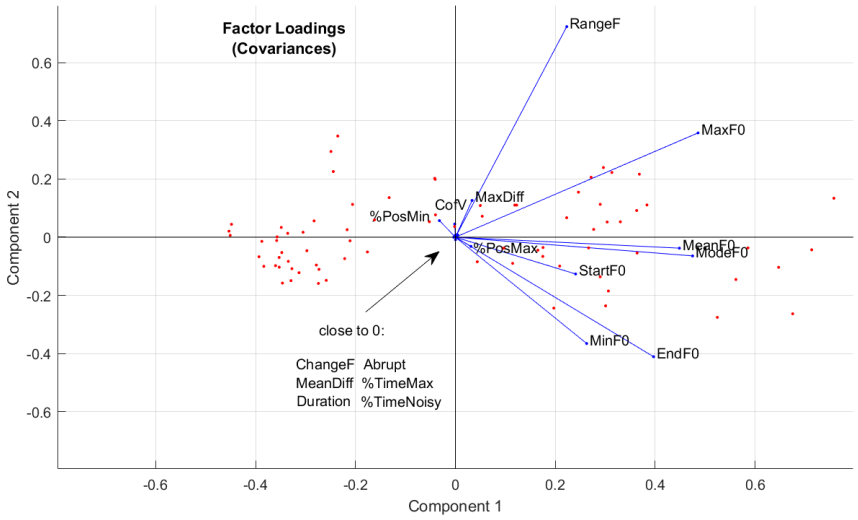

Figure 4. Plot of factor loadings for principal components. Most of the variation in the howls was described by six variables (see Table 3).

	PC1	**PC2**
MeanF0	0.4486	
ModeF0	0.4749	
EndF0	0.3967	-0.4111
MaxF0	0.4858	0.3586
MinF0		-0.3656
RangeF		0.7243
Explained	**74.0093%**	**11.5931%**

Table 3. Coefficients (eigenvectors of covariance matrix between PC's and original variables) over 0.35 are shown for each principal component retained. The last row shows the percent of the variance explained by each PC.

The first two principal components were retained. Factors loading highly in PC1, which explained 74% of the variance in the sample, included the mean and mode of the fundamental.

The minimum and range of the fundamental loaded highly in PC2, which explained 11.6% of the variance. The end and maximum frequencies loaded highly in both PCs using a threshold eigenvalue of 0.35.

Plotting the howls against PC1 and PC2 shows that there were no distinguishable clusters based on border groups, packs, months, or pre-chorus vs. non-chorus howls. No differences or discriminable categories were found in the howl data.

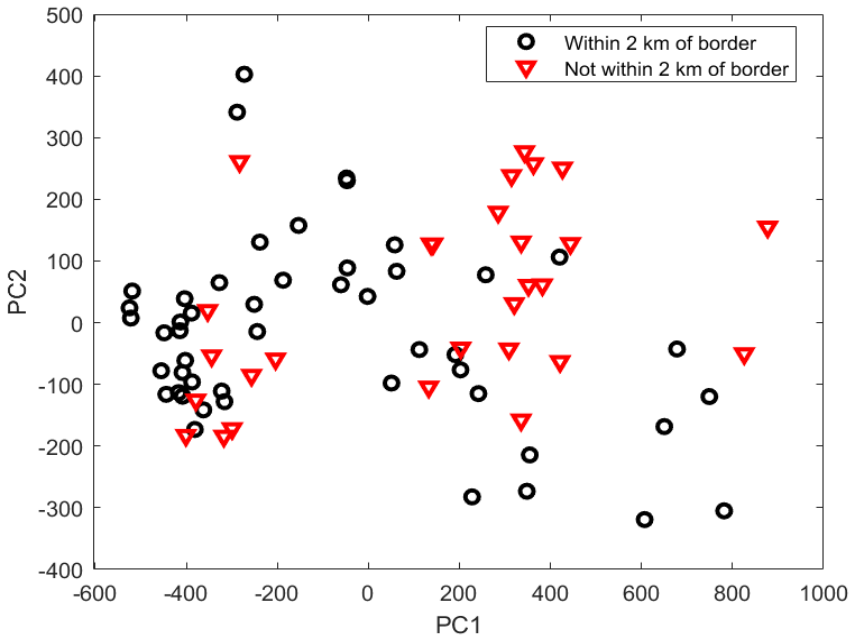

Figure 5. Howls plotted against principal components and color coded by 2km border category. Howls did not cluster by border category (1 km, 2km, or 3km), pack, pre-chorus, or month.

The lack of clustering by any of the explanatory variable groups has several possible explanations. One is that wolf howls do not differ in structure between these contexts or groups, but that conclusion cannot be confirmed by this study design either. There were many drawbacks in this study design due to the fact that the data was originally collected for a different study that was not looking at distance from borders or pack ID. For pack differences, all identifiable howls

came from two packs with overlapping territories and genetics. The recorders were not moved often enough to capture a wider variety of packs in the 2017 season.

It could still be that there are acoustic differences between howls with interpack territorial messages and howls with intrapack social messages, but proximity to a border is not a good proxy for territorial message. Especially in a region like the Northern Range of Yellowstone in early spring, with dense overlapping territories and mobile packs, territorial messaging was probably based on pack movements and activity rather than proximity to borders. Minimum convex polygons are themselves a proxy measure for the actual territories as perceived by wolves. Between the small sample size, likely pseudoreplication, and multiple layers of proxies, the ability to discover howl differences with howls recorded by passive recording is limited.

Similar studies should not only seek out a variety of packs and seasons (spring vs. fall), but also focus on observations that can be matched up with the howls. Witnessing a behavioral context is a clearer indication of a howls' possible message than any proxy variable. With sufficient observation, howls could be reliably matched to contexts such as 'carcass', 'pups', 'breeding', 'response', 'interpack interaction, 'intrapack contact', etc. Thanks to previous field studies, things like pups and carcasses could be used as proxies for territorial messaging when wolves near these resources responding to other howls. In Yellowstone, the howling individuals and their specific relationships to their interlocutors may also be identifiable. In general, while some proxies can be useful and there are important studies that can only be done in captivity, there is no substitute for extensive observation in the field with regards to identifying the context, usage, and possible message content of howls.

Why Study Wolf Communication

Relevance of Wolves to Human Language Evolution

Comparative studies of language evolution are difficult, as humans are the only species widely agreed to have true language and their closest primate relatives have relatively small vocal repertoires without productive combinatorial systems of calls (Seyfarth & Cheney 2014). Human language is partly based in social cognition mechanisms common to primates that are involved in aspects of social cognition including classification of conspecific calls, recognition of individual faces and voices, and integration of facial and vocal information. In nonhuman great apes, a homologue of Broca's area (used for speech production and processing in humans) is involved in the production and perception of facial expressions and species-specific vocalizations, and asymmetry in this area is associated with communicative gestures and vocalizations (Schenker et al 2010). Primate social groups are maintained using signals that facilitate social interactions, mechanisms used by receivers to integrate multiple sources of information (signal type, identity of signaler, previous interactions, and relationships among individuals), and the ability to assess the meaning of a sequence of events including signals that make up interactions between conspecifics (Seyfarth & Cheney 2014). Several great apes can learn communication systems invented by humans or based on a pre-existing human language. Early attempts to teach chimpanzees human language by raising them with humans from infancy failed due to anatomical constraints on speech production, but since then captive nonhuman apes have learned to communicate with humans using systems of visual symbols, including pidgin

versions of human sign languages. Humans are the only great apes who seem to have an innate grammar instinct. Human infants exposed to a pidgin can change it into a creole within a generation by instinctively applying grammar (Pinker 1994, 20-28). While it is often irrelevant to look at the performance of captive animals on tasks that have nothing to do with their normal ecology or the evolutionary pressures they would encounter in the wild, it is remarkable that closely-related great apes who live in social groups and have large neocortex sizes don't seem to approach the specificity, organization, and productive abilities of human communication.

What evolutionary pressures cause humans to further develop their social cohesion mechanisms and signals into a full language while other great apes did not? What social and ecological conditions affected humans and no other primates? Hominids joined the predatory guild at least 2 mya and intra-guild competition with large carnivores led to niche partitioning (Brantingham 1998). Bone transport patterns suggest that Plio-Pleistocene hominids filled a niche between wolves (top predators with access to organs and bone-exterior parts of carcasses) and spotted hyenas (confrontational scavengers with access to bone-interior tissues associated with head and limb elements), transporting large limb bones from newly abandoned kills (Brantingham 1998). This niche would have required strategies for resource acquisition and processing; these requirements could have been fulfilled by group foraging instead of the high-mobility adaptations of solitary scavengers and the use of hammer stones instead of cranial adaptations for breaking bone (Brantingham 1998). Hominids were hunting ungulates by the late Middle Pleistocene and niche separation within the Eurasian carnivore guild led to hominids hunted prime-aged ungulates while cursorial predators like wolves targeted old ungulates and ambush predators like lions hunted indiscriminately (Stiner 2002).

Language researchers have sometimes been reluctant to use a comparative approach based on selection pressures in different species' physical and social environments. Wacewicz and Żywiczyński (2015) examined methods of comparing communication in different species, expecting that great apes should show the most similarity with humans in all traits because they're phylogenetically closest. They were so focused on their phylogenetic expectation that all the similarities to human communication would be found in the great apes that they discounted methods of comparison that did not yield the results they were expecting. When a comparative method reveals that humans share a communicative trait with some non-apes or even non-mammals and not with other great apes, Wacewicz and Żywiczyński take that as an argument against using the method; when an approach reveals similarities between humans and other great apes, they take it as evidence in favor of using that approach because it gave them the results they expected based on phylogeny. Another effect of too much focus on phylogeny is confusing linguistic communication with the structures and faculties that provide an individual with the content for linguistic messages. Wacewicz and Żywiczyński made the same mistake as Victorian philologists in conflating communication and cognition. They discussed displacement (the ability to communicate about things distant in space and time) as an aspect of cognition (the ability to think about things distant in space and time), ignoring the different evolutionary pressures for cognition and communication. While it is true that the ability to think about something is a precondition for being able to deliberately communicate about it, the evolutionary "point" of communication is to affect the behavior of others. Cognitive prerequisites, like the ability to think about things distant in time and space, are irrelevant to language without selection pressure on the ability to communicate those thoughts to others. Wacewicz and Żywiczyński bring up

evidence for displacement in non-communicative behavior, such as corvids returning to their food caches and remembering when and where food was moved. Corvids clearly benefit from the cognitive ability to remember where their caches are, but because there is no fitness benefit to telling someone else where your cache is (in fact they go to great lengths to make sure nobody knows where their caches are so that they don't get stolen), they don't communicate among each other about the locations of their caches. While humans may think in certain ways originating in earlier primates because of their phylogeny, they are only able to talk about their thoughts because of selection on communication. It is important to compare species with similar communication needs regardless of phylogenetic closeness, and to look at species under conditions that could result in language given the necessary preadaptations[27]. A species that can think about things that are not present (because it's adaptive to be able to plan future actions) but never needs to refer to them in communication (because it's not a group-living species and its fitness doesn't rely on cooperation or coordination) is not a good place to look for communication and language evolution; we should look at species where fitness relies on cooperating and coordinating with others.

[27] If chimps and orangutans have good memories that they use to make strategic social and foraging decisions, but they don't communicate with language about those things in the wild, they must either lack some language prerequisite or are not under sufficient selection pressure to develop language. Chimps in captivity can learn to sign with useful vocabulary if not grammar (Pinker 1994), but the fact that they haven't formed their own rudimentary sign language or sign pidgin in the wild means that something is missing. It's not physical or mental ability, so it must be selection pressure—which is why just focusing on the great apes isn't the right approach for language evolution, because humans evolved in a unique environment compared to other great apes.

Human communication may have been shaped by unique pressures associated with social carnivores, so it is especially important to look at the communication of extant cooperative predators. While cetaceans are another group of mammals that utilize complex vocal communication, wolves evolved on the same landscape as early humans, dealt with the same environmental conditions, lived in groups of similar sizes, and hunted the same prey (Theberge & Theberge 1998). Nonhuman great apes do not rely on collaborative foraging and do not exhibit the resource sharing behaviors necessary for collaborative foraging situations, often sharing a resource only when it is too large or fragmented to defend and thus disincentivizing collaboration in scenarios where the resource could be monopolized by one individual. Human toddlers, on the other hand, collaborate to obtain and share food whether or not it is easily defensible by one individual, and they share resources more equitably if they were obtained by collaboration (Melis et al 2006; Hamann et al 2011 cited in Tomasello et al 2012). Preverbal humans also communicate about the collaboration, while human-raised chimpanzees do not use any signals specific to the foraging activity (Tomasello et al 2012). Human predatory behavior is nearly unique among extant primates (Stiner 2002), and humans are the only primate with a complex system of vocalizations. Clues about the adaptiveness of human language, why it evolved, and why it didn't evolve in other primates (as opposed to the cognitive mechanisms underlying it) may be more probably found in species outside of the primates that experience similar selective pressures to early humans.

Pressures on Wolf Communication from Socioecology

Hunting strategies and cooperative living are important for both humans and wolves, although there may be some differences in the functions of groups. Communal hunting is

common in wolves, as are communal feeding, sleeping, and resting, which are seen in most gregarious canid species (Smith 1977). A wolf pack usually consists of two adults (the alpha pair) who have the most experience and several juveniles who do not contribute much to the hunt (Mech & Boitani 2003), and hunting success in YNP does not increase beyond 4 individuals (MacNulty et al 2012). Pack size depends on prey size (how many wolves can feed at a carcass), not the other way around (Mech & Boitani 2003). Furthermore, in both wolves and humans, group size is not the same as hunting party size. The main evolutionary driver of group living in wolves is not the necessity of large groups to take down large prey, but the ability to share more food with offspring rather than scavengers (Mech & Boitani 2003). In humans, the need to collaborate to defend large carcasses against other scavengers may have been important in selecting for more generous and cooperative behavior around food (Tomasello et al 2012).

Cooperative hunting alone does not necessarily require complex cognitive or communicative abilities, and familiarity and kin relationships may be sufficient to reduce aggression between group members to allow cooperation, but using communication to maintain social structures and share information is beneficial to cooperation and group living (Bailey, Myatt, & Wilson 2013). The ability to form long-term social bonds and recognize relationships among others is the best predictor of reproductive success in chimpanzees and baboons (Seyfarth & Cheney, 2014). A similar mechanism is likely at work in wolves, where breeders usually require help from other adults in the pack during denning season and a lack of social bonds results in a lack of helpers (Smith & Ferguson 2012), establishing a new pack requires forming a bond with another lone or dispersing wolf (Mech & Boitani 2003), and dispersing wolves attempting to join a pre-existing pack must be able to form bonds and predict the behavior of

others. Seyfarth & Cheney (2014) argue that social cognition in primates involves "discrete elements linked—as in language—to the organization of items into concepts", such as social categories that persist through changes in membership. While wolf packs don't contain families ranked in a linear dominance hierarchy like baboon troops, and a pack is always some variation on a family group (Mech & Boitani 2003), packs persist for varying lengths of time despite changes in composition of individuals due to birth, death, immigration, and emigration. Knowledge of family relationships is also retained and combined with information about pack membership; tolerance for trespassers may be affected by the likelihood of members of neighboring packs being related, such as in Algonquin park[28] where there is a high rate of dispersal (Theberge & Theberge 1998). Group selection also acts on wolf packs separately from kin selection, as unrelated members of a pack share the same fate; like humans, they exhibit cooperative group living, division of labor, and competition with other groups (Theberge & Theberge 1998). However, as in humans, individual personality variation is important for determining the actions of individuals and packs with highly influential members (Smith & Ferguson 2012), and individual personality affinities and incompatibilities can override expectations from relatedness (McIntyre 2016).

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[28] It should be noted that the wolves in Algonquin park are properly *C. lycaon*, not *C. lupus*. *Lycaon/rufus* split from the coyote lineage and evolved in North America, as opposed to the gray wolf which evolved in Eurasia and migrated back into North America (Wilson et al 2000). They still hybridize with coyotes, including in Algonquin park (Theberge & Theberge 1998) and, like coyotes, may have more flexible social strategies than *C. lupus*. The species is often referred to as a subspecies of gray wolf (*C. lupus lycaon*), but I will use the historical classification *C. lycaon* throughout this paper to avoid construing *lupus* as a polyphyletic group (Theberge & Theberge 1998). Similarities in howl-type use also support lumping *C. lycaon* and *C. rufus* together (Kershenbaum et al 2016).

Species that are more adapted to group living are less able to afford the disruptive effects of agonistic behavior, so signals adapt to control agonistic behavior as well as to facilitate the formation and maintenance of social groups (Smith 1977). Conflict management strategies evolve to mitigate the costs of conflicts by preventing them from occurring, preventing them from escalating, and resolving them when they occur (Baan et al 2014). Conciliatory behavior for conflict resolution is rare in primates with despotic dominance relationships (which occur where within-group competition is high and between-group competition is low) and common in primates with tolerant dominance relationships (where within-group competition is low and between-group competition is high). Wolf packs are characterized by the same ecological and social conditions that favor conflict resolution in primates, and they utilize displays to prevent conflict escalation within packs (Baan et al 2014). Wolf communication involves long- and short-range vocalizations, olfactory signals, visual signals, and tactile components (Harrington & Asa 2003). Unlike solitary canids, social canid species use complicated visual signaling based on facial expressions and tail postures/movements which are important in managing agonistic interactions (Smith 1977). Within packs, postural attitudes along with short-range vocalizations like growls and whines convey information about social relationships and motivations, mediating social interaction without conflict (Harrington & Asa 2003). At long distances, scent marking and howling provide information on the location and identity of the signaler and contribute to spacing between packs and conflict avoidance. Scent marking provides additional information on both spatial and temporal distance (as the scents degrade predictably over time so a receiver can determine how long ago the mark was made) and breeding status. Scent marking is concentrated near territorial borders in both wolves and coyotes (Peters & Mech 1975, Gese & Ruff 1998) and

wolves react to scent marks near borders by leaving their own scent mark and then returning to their own territory, even abandoning wounded prey when it crosses a border (Peters & Mech 1975). In a Yellowstone coyote pack, howling was concentrated in the periphery of the territory; the periphery was 26% of the territory and the pack spent 33% of their time there, but 56% of the howling occurred there (Gese & Ruff 1998), while packs in the Białowieza Primeval Forest (where pack density is lower than in YNP and packs are not always surrounded by other territories) howled more frequently from the centers of their territories and placed less emphasis on interpack territorial howling (Nowak et al 2007).

In communication, a display is "any behavior adapted in physical form or frequency to subserve social signal functions" (Moynihan cited in Smith 1977) or as a stereotyped act specialized to make information available. It is adaptive to provide information that leads another individual to behave in a way that benefits the fitness of the signaler. Because natural selection acts on the ability of displays to elicit responses, a display is adaptive only to the extent that it causes receivers to behave in a way that is beneficial to the signaler's fitness (Smith 1977). Signals derive their usefulness from their relationship to other things (referents); a display encodes a behavioral message when it is correlated with some behavior or set of behaviors in the signaler (Smith 1977). "Message" has been defined as "information present in the signal as a direct consequence of natural selection" because at least the sender has benefitted from the evolution of the signal (Harrington & Asa 2003). The signaler influences the receiver's expectations about future events by way of the message, metainformation (such as higher vocal frequency indicating a smaller animal), and contextual information. Receivers respond based on the combined information available to them from the signal itself, the context of the signal

including the signaler's identity and reliability, past events, and remembered information—white-throated sparrows respond to tape-recorded calls from a neighbor being played from the wrong direction (not from the direction of the neighbor's territory) as if responding to a stranger (Falls 1969), and vervets responding to alarm calls often look around for additional information (Seyfarth, Cheney, & Marler 1980).

Signals include messages that are behavioral (what, how) and nonbehavioral (who, where) (Smith 1977). The function of a behavior is not the same as the function of communicating about that behavior; for example, the function of communicating about fighting is usually to avoid an actual fight, which is not the function of fighting itself. Most displays are thought to have originated as actions or parts of actions adapted for a direct function that also happened to provide information about the animal's actions (such as a snarl indicating intent to bite), and then evolved into a formalized display adapted for conveying information about the direct function; from there new displays split off and evolve from preexisting displays when it is adaptive to be able to communicate different or more specific information, leading to more diverse signal repertoires. Formalization occurs via ritualization (genetic evolution) and conventionalization (specialization by experience/learning). Repertoire size is limited by perceptual capacities, just as signal structures are limited by perceptual and ecological pressures. Different signals must be easy enough to tell apart, not too long or complex to be worth the effort for signalers and receivers, conspicuous enough to be noticed by the target audience but not so conspicuous as to attract predators and competitors, and redundant enough to be perceived in noisy environments (Smith 1977). Ritualized displays can be entirely genetically determined with respect to their structures, referents, and responses and still be classified as communication

because the signaler affected the receiver's behavior (this is what allows nest-parasitizing birds to take advantage of the hardwired response for adults to feed any chick in their nest displaying a large pink open mouth); but more complex ecological and social environments require more specialized cognitive abilities as signalers and receivers must change their communicative behavior more rapidly than they could by direct genetic evolution on the signals and responses themselves. These abilities underlie the human language faculty and are particularly important for social species with high-stakes group politics and environments that require cooperation.

Wolves often vocalize during social behavior, and the majority of vocalizations in wolves are used at short distances among packmates (Harrington & Asa 2003). At short range, these vocalizations are integrated with information from visual, tactile, and olfactory sources. Like vocalizations in many birds and mammals, they tend to follow Morton's motivation-structural rules (Morton 1977) with harmonic, higher-pitched sounds and variations occurring in friendly or submissive contexts and noisy, lower sounds occurring in aggressive and dominance contexts at short range (Harrington & Asa 2003). In a meta-analysis of 151 vocalizations from 50 mammal species, all aggressive vocalizations were lower frequency than their species midpoints while all non-aggressive vocalizations were higher (August & Anderson 1987). While aggressive vocalizations were more noisy than species midpoints, non-aggressive vocalizations were variable in noisiness (bandwidth) and did not differ significantly from species midpoints.

August & Anderson (1987) tested Morton's MS rules using two categories of vocalizations, "aggressive" (if they occurred as threats or before or during a fight) and "fear/appeasement" (submissive displays, retreat, greeting, or friendly contexts). The lumping together of fear with friendliness may have played a part in the variability of bandwidths in their

"fear" category. August & Anderson admit that fear and friendliness are "markedly different motivations", but they lumped them into a category following Morton (1977). Associating fear with friendliness would never be intuitive to a human discussing human behavior—who would be friendly with a scary individual?—but the idea may have arisen in the study of nonhuman animals alongside Victorian "red in tooth and claw" ideas about the nature of competition and brutality in the wild and been attached to a preoccupation with competitive interactions associated with the cultural milieu of particularly male researchers around the time Morton was publishing (Fausto-Sterling 1997, Lopez 1978 p.32). Barry Lopez (1978 p. 48) also pointed out that humans tend to interpret submissive gestures as "neurotic", but what we call "submissive gestures" in wolves would more accurately be called "reassurance displays" that promote group cohesion. "Humble" and "confident" have also been used to describe moods or behavioral profiles associated with lower and higher probability of conflict escalation (Packard 2003). While words like 'humble', 'confident, 'aggressive', and 'friendly' can imply certain emotional states which are not directly observable, they point to certain observable behaviors. It is confusing to base a category on an emotion which is not directly observable the way behaviors are, especially when the resulting behaviors are unpredictable. Both aggressive and non-aggressive behaviors (fighting and fleeing) can be motivated by fear, but the differences in vocalizations in this case (Morton's high frequency and harmonic vs. low frequency and noisy vocalizations) appear to be related to the type of behavior they accompany rather than the emotional state driving the behavior. If fleeing/retreating and friendliness contexts have similar vocalizations because they both occur in the broader umbrella of "social behavior that is not aggressive", then the categories should simply be labeled aggressive and non-aggressive.

Especially in a social mammal like the wolf, using language that conflates fear and friendliness could obscure humans' interpretations of observed behavior and their conclusions about the nature of social relationships. Regardless, low frequency is likely important for agonistic encounters because low vocal frequencies are associated with large body sizes, and an animal who sounds larger when making a threat display could motivate opponents to retreat.

Brady (1981) hypothesized that all canid vocalizations evolved from growls and whines, two vocalization types that most (if not all) canids have in their repertoires. Growls and whines (or a graded continuum with growls on one end and whines on the other) are very plausible as precursors, since a limited repertoire of those vocalizations would provide a noisy/low signal for aggressive messages and a harmonic/high signal for non-aggressive messages, facilitating social interaction at close range. According to Morton (1977), the selection pressures favoring these differences between friendly and aggressive sounds are produced by close proximity, although they can affect long-distance calls of animals that live in groups. Due to the danger inherent in interpack interactions between wolves and the need to predict actions like how a wolf or pack might respond to a trespasser, these pressures are probably present at long distances; but the primary selection pressure acting on howls is the ability to be heard over long distances, which constrains them to lower pitches and harmonically purer sounds, so contextual variations in pitch and noisiness based on motivation-structural rules are not likely to be found in howls. Barks are used at short range but can be heard over relatively long distances and are often detectable on the recordings. Barks consist of rapidly frequency-modulated chevron shapes, a short "intermediate" shape that indicates indecisiveness on whether to engage in aggressive or non-aggressive behavior in many birds and mammals (Morton 1977). In the case of wolves, the bark structure

should be easy to localize because canid barks cover a broad frequency range, allowing listeners to estimate distance based on relative attenuation of the different frequencies, and the short duration of a bark makes it easier to judge distance based on reverberation (Mitchell et al 2006). Barks possibly first evolved because of their ability to draw attention to the signaler (Harrington & Asa 2003). Wolf barks have also been found to vary according to Morton's MS rules along with short-range vocalizations from many other mammals and birds (Harrington & Asa 2003).

Cohen and Fox (1976) classified canid vocalizations as eliciting approach or withdrawal and on a continuum from low to high intensity. In a cross-species comparison they found that less social canids don't use mixed sounds as often as more gregarious canids and concluded that "with increasing social complexity in the Canidae, there is also an increasing complexity of the communication repertoire". Increased sociality may cause greater need to express multiple emotions at once (mixed motivations), provide a more nuanced representation of one's own affective state and possible actions, or include redundancy to ensure a message is understood. They also found in some canid species that mechanical and unvoiced sounds can be used for short-range communication, such as tooth snapping for conflict and panting for play solicitation. The full communication behaviors also include "body language" that uses postures and facial expressions, which can also be "mixed" in situations with mixed motivations or complex emotions. They compared gradations of sound types and postures/expressions to the "paralanguage" of emotional overtones in human speech, concluding that canid vocal communication was "essentially an emotional language" (Cohen & Fox 1976).

It is important for wolves to be able to communicate in ways that facilitate group cohesion, breeding, and territorial defense. Trespassing is not uncommon among wolves, and

boundaries between territories can overlap. Occasionally entire territories are redefined in events like pack splitting (Theberge & Theberge 1998), so wolves experience pressure on learning the land and the possibly changing boundaries of their own territories and those of other packs. Their defense of territories must also be flexible; if young dispersers were never allowed to travel through existing pack territories, there would be a barrier to gene flow. Judgments about resources also have to be made. A territory is nothing more than a defended home range; for territoriality to evolve, there must be competition for defendable resources, and the defense must not be too energetically costly or interfere with reproduction (Mech & Boitani 2003). But prey density can fluctuate, and with it the cost-benefit ratio of defending a territory changes (Theberge & Theberge 1998).

Physical and social environments that require flexible behavior select for cognitive flexibility and group coordination that can respond to changes. Yellowstone is a particularly interesting region because the packs are mostly protected from human exploitation but the landscape of the park and surrounding land, including the ecological and social environment of wolves, is heavily influenced by the social activities of humans. The actions wolves take to respond to this environment as individuals and packs are facilitated by communication. Further study of the specific mechanisms and possible messages of wolf communication can provide clues about associated cognitive abilities, their evolutionary history, and why they are adaptive.

CHAPTER SIX

CONCLUSION AND DIRECTIONS

It is important to understand the history of wolf-human relations in a given region in order to contextualize how people perceive wolves today. Questions and ideas about wolf communication surface and gain attention depending on their relation to paradigms in ethology, psychology, sociobiology, and the cognitive and communicative aspects of the struggle over human uniqueness. Since the beginning of research focused on wolf howls, the same questions have appeared since at least the 1960's, but methods have become more technical as humans struggle to quantitatively describe the full structure of a continuous modulated vocalization and determine which aspects of its structure may be able to encode semantic meaning.

Historians have examined how human economic situations and cultural trends are expressed in the ways in which they describe wolves and their howls. Now we need to make an attempt to disentangle the influences on humans' perceptions of wolf howls; including cultural biases, vernacular knowledge gained from observation, and instinctive responses to the percieved affective content of howls. Tracing the origins of different explanations will help us figure out how much we can trust vernacular attributions of meaning. This will involve keeping track of indigenous knowledge, vernacular science, and the evolutionary origins and adaptive characteristics of folk psychology; and determining the relative contributions of human culture, human biology, and knowledge gained from observation to these influences.

In attempting a study of possible semantic information in wolf howls from different locations within pack territories, I found that the field is in need of new ways to describe continuous vocalizations, and that there is no substitute for intensive observation when it comes

to understanding the socioecological context of howling events. In the realms of both acoustic structure and howl context, researchers need to keep Burghardt's fifth aim of subjectivity in mind and avoid anthropocentric assumptions about how wolves hear howls or how they understand a given situation. Howls and behavior must ultimately be approached from a "lupocentric" perceptual angle.

Here, I will suggest topics and research directions for students of wolf biology, human history, and wolf history. I will also address the key takeaways about what biologists and humanists can learn from each other when studying communication and behavior in a highly cultural species such as the wolf.

Topics for Future Research

In Captivity

While continuous study of wild packs is ideal, some questions are best answered using experiments on captive wolves with known identities and the ability to manipulate behavioral contexts and control for extraneous circumstances. Some of these recommended captive studies come from observations in the wild and others are continuations of previous research.

The captive Iberian wolves in Palacios et al (2015) demonstrated discrimination of howls from different individuals, but the experiment did not include an opportunity for the wolves to demonstrate individual recognition (matching between the howl and a mental representation of the howling individual), as the experimental stimuli were from howls of unknown wolves. A possible recognition study could involve removing a wolf from an enclosure and moving the wolf out of sight (and out of earshot) to elicit howling from their packmates as in Watson et al (2018), then playing recorded howls from the missing individual or howls from a non-pack wolf

to which the pack has been previously habituated. If there is a captive population including at least two packs or groups in adjacent pens, one wolf could be removed from each pen, and then the researcher could play a recorded howl from only one of the missing wolves through a speaker an equal distance away from both pens and then record the attention responses in each group. One group will be responding to the voice of a separated packmate, the other will be responding to the voice of an individual they are familiar with (from living in adjacent enclosures) but not attempting to reunite with. The nature of artificial packs in captivity might make this irrelevant or impossible at some facilities, as "packmates" may be unrelated and they may not view residents of an adjacent pen as non-packmates the way wild individuals would. It would be best if the adjacent captive packs were kin groups or at least included kin of the separated individual, so that reactions of kin could be compared. The playback howls would be recorded in a similar context (when the wolf in question was separated from the group, ideally when they were responding to howls from the group elicited by their removal) prior to the trials. Another option is to use the findings of Mazzini et al (2013) which showed that captive wolves howl more when attempting to locate a wolf with whom they have a strong affiliative relationship. An experiment could involve removing a popular or dominant wolf as well as a random, less popular wolf to somewhere out of earshot of the rest of the group. With both wolves missing, play back a howl

from one of the two wolves. If the more popular wolf's howl gets more responses[29], this would provide evidence that the other wolves use the ID information in howls to respond appropriately.

One captive experiment that could guide future research on howls and behavioral contexts would be a habituation-dishabituation experiment like that described by Palacios et al (2015) to answer the question of whether wolves discriminate between howls produced in different contexts. Instead of changing the individual, stimulus howls would be recorded from the same individual (possibly a captive wolf from another facility) and the experiment could test for discrimination between spontaneous howls and howls elicited by removal of a group member (the two contexts found to be discriminable by Watson et al). Later tests could discriminate between more pairs of contexts such as 'elicited by removal of group member' vs. 'elicited by playback', and then more specific contexts recorded in the wild like 'recorded at a carcass after a successful hunt' and 'recorded after the death or disappearance of a pack member'. One could also compare how rapidly they habituate to a new howl from the same individual in the same context as opposed to a new howl from the same individual in a different contexts. If captive

[29] Mazzini et al (2013) did not use generally popular wolves, but assessed the affiliative relationships between pairs and only counted howls from certain individuals to assess against their relationship with the missing individual; it may be more accurate in this proposed experiment to replace "popular" with "strongly affiliated" and to score responses separately for each individual in the remaining group according to their relationship to the missing wolf whose howl was played. Playback stimuli should be recorded under similar conditions (removing the wolf and recording the howls they use to contact their packmates when out of sight). Ideally, captive groups used in this kind of experiment should have structures similar to those of real packs to accurately simulate social relationships in the wild (the pack should be composed primarily of parents and offspring).

wolves do not show discrimination between contexts of howls in the absence of context cues, it may be futile to compare the structures of howls from different contexts in the wild[30].

Also following Watson et al (2018), an identical analysis could be done which replaces the "elicited by removal of a group member" category with "elicited by playback". The type of playback stimulus could also be varied to see if wolves howl differently in response to recordings of howls from one unfamiliar wolf, a chorus from an unfamiliar pack, and one or more humans howling. Many wild studies have studied response in terms of the number of howls or howling bouts elicited by a stimulus, but these responses should also be analyzed in terms of howl structure; due to the difficulty of recording in the wild[31], it is reasonable for these questions to be asked first in captivity. Another advantage of captivity is that saliva samples can be taken for cortisol analysis, allowing one to control for stress when comparing howl structures. The same experiment as Mazzini et al (2013) could be repeated using acoustic variables of elicited howls to compare responses to the removal of different individuals with different affiliative relationships to the howler. Where Mazzini et al merely counting the number of howls elicited, this experiment would ask if wolves use different howls when looking for missing packmates with different affiliative relationships to the howler (controlling for stress/cortisol).

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[30] It could be that the diminished set of possible contexts in captivity means captive wolves would not respond to or be aware of differences between howls recorded in wild contexts, or it could be that caller ID, location, and known context clues are sufficient for wolves to interpret the meaning of howls and wolves do not need to include specific semantic information in their long-distance vocalizations. We know there are structural differences between at least two howling contexts (Watson et al 2018), but it is unclear whether those differences represent differences in semantic content, arousal, affective valence, or all of the above.

[31] For example, while Root-Gutteridge et al found that amplitude modulation may encode information in howls, amplitude variables from the Yellowstone recordings in this study could not be used because of long distances and.

Non-harmonic aspects of howling can also be assessed in captivity (along with short-distance vocalizations which are mostly unavailable for study in the wild). Tooze et al (1990) found that noisy bands in howls were related to individual differences, but they did not know whether these differences were related to individual rank or territoriality. Noisy bands at the end of howls were found to be more territorial than noisy bands at the beginning or middle (Tooze et al 1990), but noisiness in other parts of the howls which is correlated with individual ID may reflect individual rank, competitiveness, or territoriality rather than a constant aspect of individuals. In captivity, noisy aspects of howls can be recorded accurately and individual personalities can be more closely observed. That would allow one to check for correlation between noisy bands in howls and individual competitiveness or current rank (especially if an individual's rank changes and their howls subsequently become more or less noisy).

Captive wolves could also potentially be used to estimate what proportion of chorus howls are picked up by recording units in the wild by measuring the rate of spontaneous chorus howls in captivity during different seasons, adjusting for pack size (Harrington 1989), and comparing it to what is recorded in the wild—although it could be that one should expect more choruses in the wild because some "spontaneous" choruses may be elicited by hearing other packs or even heterospecific noises, and those stimuli may not exist in captivity. Audio-recording collars like those used to record incidental sounds in mule deer by Lynch et al (2013), adapted for use in wild wolves to smaller recording units that can be mounted on radiocollars, could provide better information on this and other questions about howling behavior in the wild.

In the Wild

Regardless of how many captive studies are conducted and how thorough the research on captive wolves is, wild observations are required to place the findings in evolutionary context, and there will always be some questions that can only be answered in the wild.

Because wild wolves regularly hear howls from neighboring packs and are involved in territorial maintenance, they are candidates for playback studies assessing whether they recognize howls from their neighbors by comparing their responses (including howling, attention, and movement toward or away) to playbacks of howls recorded from individual in neighboring packs and from completely unfamiliar wolves. While captive wolves can have neighbors whose howls they recognize, they are not subject to normal territorial conditions and may not respond in relevant ways. They also might show responses that would not appear in the wild. Harrington (1989) said that individual ID may not be discernable over interpack distances because of signal degradation. If this is true, wolves may only use the individual ID information in howls when communicating within their own pack. Captive wolves hearing the howls of a stranger in a playback study may react differently than wild wolves who may not be able to tell if a howl from a long distance away belongs to a stranger or a packmate. At the very least they should be able to tell something about the howler's size from the howl's frequency[32]. Playback experiments should compare responses to the howls of strangers, neighbors, and packmates;

[32] Another playback question: do wolves respond differently to playbacks from larger and smaller wolves? How do the results compare to studies or their responses to human howls such as that of Harrington & Mech (1978)?

these should be played at short (intrapack) and long (interpack) distances, for a total of 6 treatment conditions. Responses could indicate whether the wolves recognize their neighbors' howls as different from stranger howls (even if individual ID information is not available over long distances, they may have some experience with hearing neighboring packs from shorter distances) and if they can identify familiar howlers from long distances.

Questions about whether wolves can hear and interpret differences in howls from different contexts can also be brought into the wild. For example, if territorial howls aimed at competing packs are found to be acoustically different from howls aimed at packmates, howls from both contexts (interpack and intrapack) could be recorded from one pack and then played back to a neighboring pack to see if the neighbors respond differently. Howls recorded at a kill site could be played in another location to see if listeners respond by attempting to go toward the presumed location of the carcass—this would be an investigation of howl meaning as well as historical vernacular claims that wolves have a specific howl used after making a kill which can function to call scavengers to a carcass. If it sounds like one trespasser at a kill within a resident pack's territory, do they approach? Are eavesdropping scavengers more likely approach the playback location if the howl stimulus was recorded at a kill than if it was recorded in another context? Because howling after a kill is likely used to regroup after wolves were separated while hunting, or to summon other pack members who were not in the hunting party to the carcass, the control stimulus for this kind of playback experiment should be from the context of a pack regrouping or gathering its members in the absence of a carcass. If these howls prove to be different than howls made to gather pack members at a carcass (by acoustic variables or listener responses), then there would be evidence that some howls may contain a food-related message.

Another question that can only be answered in wild packs is that of group vocal signatures: do individuals from the same pack have howls that are more similar to each other than you would expect from genetic relatedness alone? Zaccaroni et al (2012) found vocal differences in packs that seemed to be related to geography and dispersal, but they could not control for relatedness or multiple howls from the same individuals. Watson et al (2018) examined three captive packs at the same facility, using a nested pDFA to control for multiple contributions from the same individuals, and could not discriminate howls into packs. However, the "packs" in captivity had artificial structures, and the pups were human-reared which likely inhibited opportunities for social learning of vocalizations from parents and other relatives and packmates. Watson's findings could indicate that there are no pack signatures besides similarity that comes from relatedness, or that all howls from that facility grouped together into one effective "pack" because of proximity. Using packs with well-documented genealogies like those in Yellowstone, one can record howls (with visual observation so individuals can be identified) and then look at the similarity of pairs of howls within a pack compared to pairs of howls from different packs, while controlling for known relatedness between pack members. Another way to examine group signatures vs. relatedness is to record howls from siblings who dispersed and those who did not. If dispersed individuals sound more like other members of their current pack than their siblings do, or if siblings living in the same pack sound more similar to each other than they do to their siblings who dispersed and now live in different packs, there would be some evidence for group signatures or culturally developed vocal patterns. Ideally a group of siblings would be recorded over time starting before any of them dispersed; then whenever one of the

siblings disperses, their howls can be sampled over time along with their remaining siblings to see if their howls become less similar to their siblings' over time.

It is also not clear that relatedness causes similarities in howling on an individual scale (individuals may develop their own characteristic howls independently of genetics). Pairwise comparisons of howls from captive wolves from the same facility, some related and some unrelated, could clarify this question (do the howls of siblings group together more closely with each other than they do with howls of unrelated wolves from the same facility or artificial "pack"?). Similarity of howls within packs that are differently related could also be compared (such as a pack made of only parents and offspring that are full siblings vs. a pack with a stepparent, half-siblings, and unrelated dispersers).

Mitchell et al (2006) found individual ID information in coyote barks and howls. Most of the howl variables important for individual ID in coyotes were things that should be under voluntary control and not just a function of larynx morphology: duration of fall, slopes of different parts of the howl, and presence of wavers. If a lot of individual-ID related howl features are about voluntary control and not genetic larynx shape, then are they more likely to be subject to cultural change as individual modify their howls to fit in with a social group? Should we expect to find cultural trends in howling within packs or populations? Has immigration ever caused a 'revolution' like in humpback whales by introducing a new howling trend to a population, or is that only possible with song because of the variability of calls with a combinatorial structure?

Kershanbaum et al (2016) found that larger species used howls with less frequency modulation, particularly at the end of the howl, but pointed out that "this may be an artefact of

the lower fundamental frequency used by larger species". A similar study looking at different body sizes within the same species could reveal whether the difference in frequency modulation at the end of the howl is actually just an artefact of body size or if it's species-specific.

The study I attempted in this paper suffered primarily from small sample size (most howls were probably not captured by the stationary recorders) and unknown howling contexts, which forced me to use location and month as proxies which may not actually correlate to howling contexts or meanings. Recording howls while radiotracking like Nowak et al (2007) would allow researchers to pick up as many spontaneous howls as possible. It would also provide the ability to identify the social contexts and functions of most howls, as humans would be able to observe the wolves' movements and activity. Then a PCA and DFA could be applied to see if these howls could be accurately classified into social contexts based on acoustic variables alone.

Given the howling contexts Nowak et al (2007) observed, analyzing howl structure with respect to context could be useful for predator-prey studies. If structural differences are found between howls produced in all these contexts, determining what kind of howl indicates a fresh kill could aid in the estimation of kill rates in forested areas with low visibility by providing a proxy for actually seeing a kill, and the ratio of "setting off on a hunt" howls to "fresh kill" howls may provide a proxy measure for hunting success (depending on the specific functions and factors that cause wolves to howl or not to howl in these contexts; if pre-hunt howls and fresh-kill howls serve to gather packmates together, or if they are released by an emotional state which builds up from interactions between individuals, they may be uncommon in small packs that are rarely separated).

Harrington and Mech showed that packs will respond to howls from strangers (as the packs in their study area treated human howls as if they were unknown wolves) at a higher rate when they are near a defended resource (like kills and pups) and when the strange howl is coming from inside of the pack's territory. It is possible that spontaneous territorial howling from the interior of a territory is rare and unrelated to the response rate to human howling that appears to be coming from an unknown trespasser. In one Polish population, all recorded spontaneous howls were from the interior of pack territories, and most of these howls occurred in intrapack social contexts (Novak et al 2007). More howling data from wild wolves must be collected before any general claim of this nature could be defended. Recording units would need to be placed in the buffer zones as well as territory interiors, and they must be spread over a wide enough area covering multiple pack territories to pick up any howls that wolves in the target pack(s) may be able to hear so that researchers will be able to discriminate between spontaneous howling and responses to other howls. Where playback studies are possible, recordings of howls from individual wolves could be played near the border and inside the territory of another pack to elicit the responses a pack would give to a known neighbor in different locations (buffer zone, trespassing, etc.) as opposed to the human howls or recorded captive wolves used in previous studies, which the packs would have treated as totally unknown intruders.

While accessible populations like the Yellowstone wolves continue to be invaluable for long term research, observational studies in isolated regions are also important. Wolves that have never been exposed to humans do not see them as a threat, and are willing to demonstrate their full range of social behaviors in front of human observers. When National Geographic photographer Ronan Donovan did a project on Ellesmere Island with a population of wolves that

had never been exploited by humans, he found that they were very tolerant of humans (willing to relax and act normally in the presence of humans in close proximity) and of human objects. While Yellowstone wolves are wary of camera traps outside of their homesites, the Ellesmere Island wolves were not afraid of a camera placed inside the den. Such populations represent an ideal opportunity to witness normal social interactions and to record short-range vocalizations with their full behavioral contexts.

Yellowstone Questions

Hunting strategies that are learned and passed down culturally are probably important in Yellowstone, as only some packs hunt the more challenging prey in the park. Interpack competition may also rely on learned strategies; success in territorial interactions relies on not only group size but the presence of experienced individuals, especially older males (Cassidy et al 2015). As for hunting, larger packs are more successful at hunting bison, but group composition and hunting success with difficult prey has yet to be examined in Yellowstone (MacNulty et al 2014). No bison were killed in 1995 or 1996. Two of the 41 reintroduced wolves had been exposed to bison before the reintroduction into the Druid Peak pack, but between 1997 and 1999 only 1 of the 14 bison killed by the reintroduced wolves was killed by the Druids (Smith et al 2000). The other packs quickly learned to kill large, difficult prey without being taught, although later the Northern Range packs largely stopped going after bison as they were exposed to a year-round supply of a preferred and easier prey (elk). The main pack that kills bison today, the Mollies, are descended from the Crystal Creek pack which killed 4 bison during ‘97-’99. It will take more observations from the ground and possibly from the air to determine whether any Yellowstone packs have unique cultural hunting strategies like the packs in Denali. What, if

anything, is unique to YNP? Are there cultural phenomena in YNP that can be traced back to the Canadian source populations, or are they recently adapted to the Yellowstone landscape? One social phenomenon that may be cultural is multiple breeding females in one pack: this is rare in most populations but fairly common in Yellowstone. Is this only controlled by prey availability, or is there a cultural element?

Many questions involve comparing Yellowstone wolves to wolves from other places and other packs within the park. Howl comparisons between Yellowstone wolves and the Canadian source population could show if there has been a genetic or cultural divergence in howl characteristics since the reintroduction. Comparisons in howling frequency and usage (as well as acoustic features) between the Northern Range and the interior of Yellowstone could show if howling is affected by the increased territorial competition in the Northern Range. Hunting strategies can be compared between Yellowstone and other wolf populations to see if there are any particular learned behaviors specific to the park's geography or the combination of being protected and heavily traveled by humans.

The accessibility of relatedness information in Yellowstone also provides opportunities to investigate behavioral flexibility with respect to kin, including differences in territoriality between neighboring packs that share related members vs. packs that are not related to each other. With enough recordings of howling events with concurrent observations with positive individual ID, howl structure could also be examined for effects of genetics or learning at the pack or family level.

There are also questions about wolves and other species in the park. Some humans believe Yellowstone coyotes howl more like wolves than other coyotes and speculate that

coyotes howl more like wolves to promote spacing between themselves and wolf packs. For a sort time after wolves were reintroduced, they killed a lot of coyotes. To my ear, coyote howls in the park sound no less "yippy" than other coyotes, but frequencies and the average amount of modulation could be compared between Yellowstone coyotes and other coyotes. Recordings of Yellowstone coyotes from before the reintroduction could also be compared to recordings from the present to see if there was a change in the way Yellowstone coyotes howl following reintroduction of wolves, whether or not the change was in a wolfward direction.

History Questions

A full treatment of the question of amateur knowledge would include archival research and interaction with and observation of wolf watchers and biologists. The emergence of different kinds of questions about wolves should be located in time and space, and historians should look for current sites of vernacular knowledge creation and compare their questions, conclusions, and methods of fact-making to those of wolf biologists. It should also include indigenous knowledge creation as an aspect of vernacular science. Information about wolves and historical wolf-human interactions can be found in oral histories and especially in the vernacular knowledge of hunting cultures as Stephenson & Ahgook described. Hunters (especially in the north where wolves are not hidden from view by trees) have both extensive experience seeing wolf behavior in the wild and a vested interest in paying attention to the wolves' hunting strategies and learning what indicates information important to humans hunting the same prey.

One human project that would be interesting is a sociological comparison of wolf watchers in Yellowstone with wolf watchers in other places and other animal watcher groups in Yellowstone. Do they have different cultures? Do their watching habits differ beyond what is

expected due to differences in geography or species of interest? How do hierarchal tendencies or cliquishness in a group of humans influence the interpretations of animal behavior coming out of that group? How do different groups of wolf and other animal watchers treat famous individuals (including famous wolves as well as famous biologists and rangers)? Is fact-building by accumulation of a volume of anecdotal observations occurring in some or all of these places? What makes a group of watchers in a given park or region more or less likely to become a site of vernacular science?

Full inclusion of wolves in the narrative of the West and Yellowstone in particular will involve an account of the wolves' cultural history and how it interacts with cultural changes in humans. Studies of this nature would continue where Coleman and Walker left off. Historians and biologist shave noted that the human cultural behavior of poisoning carcasses led to a learned behavior in wolves of abandoning carcasses, avoiding scavenging, and only eating fresh kills. Wolves in the present can only be directly compared to other extant populations, but they may be indirectly comparable using human writings and oral histories. With enough background knowledge of how to disentangle the effects of human culture and urban legends (such as the rumor that wolves hamstring their prey) from historical accounts, we can use human accounts over time to trace changes in wolf culture in certain areas. This should be combined with present-day observation, using ethological and cultural-anthropological methods, for comparative purposes and to look for cultural changes in wolf packs as they happen.

Approaches to wolf communication from a humanist angle should include going through archives for mentions and descriptions of howls and other communication combined with an observational approach watching or hearing wild wolves interact in context. Explanations of how

wolves are affected by different conditions will come from comparing wolf behavior in remote places like Ellesmere Island and human-dominated places including parks and rural unprotected areas in North America, Europe, and Asia. Observations can then be put into context with humans' descriptions from different times. When were humans in Minnesota or Montana encountering wolves that behaved more like the remote wolves of today? Is there evidence that European wolves changed their behaviors in human-dominated areas when animal agriculture took over? Can we identify a network of changes in one location, such as Yellowstone, and describe how shifts in human culture, changes to the landscape, and changes in wolf culture fit together and alter each other over time?

How to Proceed

This thesis has implications for biologists and humanists interested in questions of communication and animal history. It also speaks to our place within wolf-human relationships. Biologists continue to come up against historical forces like culture and individual personalities within changing environments while historians and humanists incorporate insights from animal studies to explain where nonhuman animals fit into power structures and historical narratives. As research on all fronts becomes increasingly multidisciplinary, the American West finds itself at the intersection point of biological, economic, and social forces leading to a resurgence of the War on Wolves.

Wolf researchers should keep in mind the importance of ethological observation and centering the evolutionary context of communication events. In questions of cognition, subjectivity, and meaning, biologists should not fear the specter of anthropomorphism as long as

the questions are based on observations and about the animals on their own terms. Long-term observation is needed for communication questions both to understand the full context and to determine hypotheses about semantic content or functional reference. Howl research should looking for better ways to accurately describe continuous vocalizations, and follow Hauser's suggestions regarding the identification of meaningful units. This is a perceptual question that must be pursued simultaneously with investigations of functional reference. These recommendations also have corollaries for non-biologists. Funders should extend financial support to more long-term observational studies. Nature writers should spend more time observing scientists rather than making assumptions about what the scientists perceive as anthropomorphic (such as attributions of specifically phrased thoughts and meanings) and what they see as allowable and not anthropomorphic (such as discussions of thoughts, emotions, or semantic symbols in general).

Many biologists who study wolf behavior have noted that wolves can use learned, culturally transmitted information about hunting. Methods used by animal behaviorists to detect and describe cultural transmission should be combined with anthropological and historical methods developed for studying humans. The socioecology of long-lived wolf packs or populations can be studied from a cultural angle by borrowing methods from humanist disciplines made to account for the effects of the physical environment on culture and learning.

When developing hypotheses, wolf biologists should not only use their own observations but also look for sites of vernacular knowledge production inside and outside of science—keeping in mind that professional researchers engage in vernacular science too whenever they know something from experience but haven't proven it scientifically or published it, but are still

confident enough to pass the knowledge down within their field. Biologists tend to discount vernacular knowledge as being too contaminated by human culture to be informative. While vernacular accounts of animal behavior are heavily influenced by culture (as scientific accounts are influenced by cultural trends such as cognitive ethology, Morgan's Canon, and behaviorism), most of these conclusions are ultimately built on observations and the nature of the observations may be discernable with knowledge of the relevant cultural trends and information from one's own field observations.

Humanists should investigate not only the cultural factors but also the biological factors influencing how humans describe animal behavior and communication. When including animals in historical research, they should step into the field and so some of their own observation. They should also locate past and present sites of vernacular science and describe their internal cultures and what kinds of facts they produce.

Wolves and other animals should be given historical agency and included in histories as actors rather than props. This means they cannot be written as landscape features when they were live animals performing actions that influenced historical events for both wolves and humans. The historical narrative is where risks of anthropomorphism arise; writers should be careful not to project intentions onto wolves that they are used to talking about when humans are the subjects. This includes the tendency of some to talk about the war "between" humans and wolves and write as if wolves made strategic attacks on humans or livestock as part of a two-sided war.

Historians should mine the archives for incidental references and see if any patterns emerge among all mentions of wolves or wolf howls, mentions from different times, or from

different voices (as different kinds of people spend a lot of time outside in wolf habitat for different reasons, and those differences affect what they notice and what they record). When discussing how humans see wolves, historians should not lose sight of their best approximation of how wolves see themselves. The wolf as a symbol in human culture and the wolf as an animal are separate, but they do interact—the symbolic wolf influences what humans do, which changes the environment of the real wolves, which in turn leads to changes in the wolves as animals that can alter the wolf as created by humans. In Yellowstone, it is important examine how human cultural events and shifts have created and changed the park itself and how this changes the selective environment for wolves. The Yellowstone wolf packs have a specific history and there may be new cultural traits shaped by the park's unique configuration of geography, prey distribution, protections and lack thereof from human hunting, park infrastructure, the YWP, and the human part of the social environment.

Finally we arrive at the current moment in our relationship with wolves in America. In February 2021, Montana governor Greg Gianforte killed a Yellowstone wolf just ten miles outside the park. 1155M was born in the park in 2014 and collared in 2018 after joining the Wapiti Lake pack. Despite the trapping location being well within the expected range for Yellowstone-based wolves, Gianforte's actions would have been legal if he hadn't skipped the required online trapping certification course. The existing laws in the state already fail to protect Yellowstone's wolf packs by attempting to reify the ecologically meaningless boundary of the national park. In addition, Gianforte recently signed two bills into law allowing snares to be used for wolf trapping (and the inevitable snaring of non-target species) and extending the wolf

trapping season. Another bill prohibits the Fish and Wildlife commission from restricting wolf hunting in areas adjacent to national parks. Bills allowing private organizations to reimburse hunters and trappers for costs incurred from killing wolves, directing the FWP to reduce the wolf population in Montana, and allowing baits, night hunting, and unlimited harvests for wolf license holders are rapidly making their way through the legislature.

While the proponents of these bills cite elk management and livestock protection, these arguments were debunked during the last iteration of the wolf war. Montanans know from the events of the 1910's-30's that elk herds without wolves suffer from overgrazing, starvation, and disease, and that human hunters cannot make up for a large decline in the wolf population. They are also aware that killing wolves on ranches leads to increased depredation on livestock (Wielgus & Peebles 2014). What forces are really behind this round of anti-wolf legislation? Once again, the wolf war cannot be explained by ecological competition alone, but it can be explained by political drives. The idea of borders is important for explaining these events. First there is the border of the national park, an invisible line meaningless to wolves but accepted and continually reinforced by humans within a political paradigm that gives significance to the boundary. This partly corresponds to the border between human and wild or inside and outside—buffer zones around the park which would reflect the socioecological realities of wolves would mean blurring the lines between civilization and wilderness to humans, threatening the idea that they are free to dominate nature as long as they stay out of certain isolated areas. Another clue comes from a seemingly unrelated act of Gianforte: signing a bill that outlawed sanctuary cities in a state where none exist. This symbolic act was aimed at anxieties over illegal immigration, which in America is driven by racism, nationalism, and blame for economic tensions such that

citizens feel reassured rather than controlled when their governments aim to control the geographic movements of humans. The persistent embers of manifest destiny lead the descendants of European colonists to feel entitled to political domination of landscapes, wildlife, and people. The border here is another incarnation of the inside/outside dichotomy, drawn between a powerful ingroup and the 'other'. Despite the progress of biological research and curiosity about wolves for their own sake, wolf-as-symbol seems to have survived and surfaced again in a continuation of the wolf war. Wolves remain a scapegoated 'other' and continue to be used as a surrogate for human 'others' into the 2020's[33].

Understanding of the intersecting arcs of culture, politics, and history that determine human behavior toward wolves often falls to historians and humanists, but their conclusions must be positioned within the findings of biologists and vice versa. It is important for ethologically-inclined humanists and historically-inclined biologists to be involved in the decisions that humans make about land, wildlife, and predators. Knowledge of the cultural and biological history of wolves can help historians conceptualize wolves as actors and agents, and a humanist approach can help biologists follow in the footsteps of Rosalie Edge and the ECC and avoid the fear of prescriptivism and involvement in contemporary political discourse.

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[33] This phenomenon is explicit in a photo from 2013 in which a group of Wyoming hunters pose in KKK masks while holding up an American flag and a dead wolf (removed from the federal endangered species list in 2011). https://howlingforjustice.wordpress.com/2013/10/28/sorry-but-wolf-slaughter-is-not-american-by-james-william-gibson/#jp-carousel-24335

A complete understanding of wolves, wolf communication, and wolf-human history requires a multidisciplinary approach with ample exchange of methods. Historians must become ethologists and venture into the field to make observations of wild wolves in their evolutionary context from a cultural perspective. Biologists must become historians and look at the history of wolf communication research in its cultural context within humans. They must also look at wolf behavior itself in a wolf cultural context, as the product of evolutionary and social processes comprising a historical process. Both approaches can benefit from many hours of observation and dialogue with sites of vernacular knowledge, both current and historical, for hypothesis formation and hints about wolf behavior and wolf-human relationships over time. The wolf should be approached in all research as an animal shaped by the socioecological pressures of cooperative hunting, packs as a unit of group and kin selection, and a strong reliance on learning from experienced group members. Whether or not howls turn out to contain detailed semantic meaning, it will be worth further investigation to describe the evolutionary history, mechanisms, and cultural components of social communication among wolves. Using a cross-disciplinary perspective, approaching questions from multiple directions, and evaluating how every event is situated in space and time with respect to cultural, ecological, evolutionary, and historical forces can lead to a fuller understanding of the character of wolves and how to confront the task of changing wolf-human relationships now and in the future.

REFERENCES CITED

"An Act to provide for the extermination of wolves and coyotes by inoculating the same with mange, and to place such duties under the charge of the State Veterinarian, and to make an appropriation for such experiments" H.B. 251, Ninth Regular Session of the Legislative Assembly, Montana (1905).

Agriculture Appropriation Bill: *Hearings before the Committee on Agriculture.* House of Representatives, 64th Congress, First Session on Bureau of Biological Survey (1916). Washington: Government Printing Office.

Aiello, Leslie C. and R. I. M. Dunbar (1993). "Neocortex Size, Group Size, and the Evolution of Language". *Current Anthropology* 34:2, 184-193.

Allen, Colin and Marc Bekoff (1997). *Species of Mind: The Philosophy and Biology of Cognitive Ethology.* Cambridge: MIT Press.

Andics, Attila, Márta Gácsi, Tamás Faragó, Anna Kis, and Adám Miklósi (2014). "Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI". *Current Biology* 24:5, 574-578. doi: 10.1016/j.cub.2014.01.058

Asquith, Pamela J (1997). "Why anthropomorphism is not metaphor: crossing concepts and cultures in animal behavior studies". in *Anthropomorphism, Anecdotes, and Animals* ed. Robert W. Mitchell, Nicholas S. Thompson, and H. Lyn Miles, 22-34. Albany: State University of New York Press, 1997.

August, Peter V. and John G. T. Anderson (1987). "Mammal sounds and motivation-structural rules: a test of the hypothesis". *Journal of Mammalogy* 68:1, 1-9. DOI: 10.2307/1381039

Ausband, David E., Sarah B. Bassing, and Michael S. Mitchell (2020). "Environmental and social factors influencing wolf (*Canis lupus*) howling behavior". *Ethology* 126:9, 890-899. DOI: 10.1111/eth.13041

Baan, Candice, Ralph Bergmüller, Doulas W. Smith, and Barbara Molnar (2014). "Conflict management in free-ranging wolves, *Canis lupus*". *Animal Behaviour* 90, 327-334. https://doi.org/10.1016/j.anbehav.2014.01.033

Bailey, Ida, Julia P. Myatt, and Alan M. Wilson (2013). "Group hunting within the carnivora: physiological, cognitive, and environmental influences on strategy and cooperation". *Behavioral Ecology and Sociobiology* 67:1, 1-17. DOI: 10.1007/s00265-012-1423-3

Bailey, Vernon (1930). *Animal Life of Yellowstone National Park*. Springfield: Charles C. Thomas Publisher.

Baldes, Richard (1995). “The Wolf as a Fellow Hunter”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 280-286. Stillwater: Voyageur Press, 1995.

Balluta, Andrew (1992). “Tigin Sutdu’a: Wolf Story”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 270-278. Stillwater: Voyageur Press, 1995.

Bark, Rusana, Annika E. Stenberg, Maoli Duan, Konstantin Yakimchuk, Anders Fridberger, Lena Sahlin, Jan-Ake Gustafsson, and Malou Hultcrantz (2009). “Inner ear pathology and loss of hearing in estrogen receptor-deficient mice”. *Journal of Endocrinology* 201:3, 397-406. DOI: 10.1677/JOE-09-0060

Bekoff, Marc (2002). *Minding Animals*. New York: Oxford University Press.

Bekoff, Marc (2007). *The Emotional Lives of Animals.* Novato: New World Library.

Blumstein, Daniel T. and Kenneth B. Armitage (1997). “Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls”. *The American Naturalist* 150:2, 179-200. https://doi.org/10.1086/286062

Bowers, Alfrew W. (1992). *Hidatsa Social and Ceremonial Organization.* Lincoln: University of Nebraska Press.

Bowler, Peter J. (1983). *Evolution: The History of an Idea*. Berkeley: University of California Press.

Bowman, Elbert F. (1938). “Wolves: Being Reminiscent of My Life on an Eastern Montana Ranch”.

Brady, Charles A. (1981). “The vocal repertoires of the bush dog (Speothos venaticus), crab-eating fox (Cerdocyon thous), and maned wolf (Chrysocyon brachyurus)”. *Animal Behaviour* 29, 649-669.

Brantingham, P. Jeffrey (1998). “Hominid-Carnivore Coevolution and Invasion of the Predatory Guild”. *Journal of Anthropological Archaeology* 17: 327-353.

Burghardt, Gordon M. (1997). “Amending Tinbergen: A fifth aim for ethology”. In *SUNY series in philosophy and biology. Anthropomorphism, Anecdotes, and Animals* ed. Robert W. Mitchell, Nicholas S. Thompson, & H. Lyn Miles, 254–276. Albany: State University of New York Press.

Burghardt, Gordon (2013). “The Janus-Faced Nature of Comparative Psychology - Strength or Weakness?” *Evolutionary Psychology* 11:3, 762-780. DOI: 10.1177/147470491301100317

Byrne, R.W. and A. Whiten (1985). “Tactical deception of familiar individuals in baboons (*Papio ursinus*).” 33:2, 669-673. doi:10.1016/s0003-3472(85)80093-2

Cameron, Evelyn (1894). 1894 Diary of Evelyn Cameron. Montana Historical Society Research Center via Montana Memory Project.

Cameron, Evelyn (1895). 1895 Diary of Evelyn Cameron. Montana Historical Society Research Center via Montana Memory Project.

Carhart, Arthur H. and Stanley P. Young (1892). *The Last Stand of the Pack*. Reprint ed. Andrew Gulliford and Tom Wolf. Boulder: University Press of Colorado, 2017.

Cassidy, Kira A., Daniel R. MacNulty, Daniel R. Stahler, Douglas W. Smith, and L. David Mech (2015). “Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park”. *Behavioral Ecology* 1-9. doi:10.1093/beheco/arv081

Cheney, Dorothy L. and Robert M. Seyfarth (1988). “Assessment of meaning and the detection of unreliable signals by vervet monkeys”. *Animal Behaviour* 36, 477-486.

Clucas, Barbara A., Todd M. Freeberg, and Jeffrey R. Lucas (2004). “Chick-a-dee call syntax, social context, and season affect vocal responses of Carolina chickadees (Poecile carolinensis)”. *Behavioral Ecology and Sociobiology* 57, 187–196. DOI: 10.1007/s00265-004-0847-9

Cohen, J. A. and M. W. Fox (1976). “Vocalizations in wild canids and possible effects of domestication”. *Behavioural Processes* 1, 77-92.

Coleman, Jon (2004). *Vicious: Wolves and Men in America.* New Haven: Yale University Press.

Cook, John R. (1907). *The Border and the Buffalo: An Untold Story of the Southwest Plains.* Topeka: Crane & Company.

Corballis, Michael (2003). “From mouth to hand: gesture, speech, and the evolution of right-handedness”. *Behavioral and Brain Sciences* 26:2, 199-208. DOI: 10.1017/S0140525X03000062

DeBlieu, Jan (1992). “A song for the Smokies”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 366-374. Stillwater: Voyageur Press, 1995.

Denevan, William M. (1992). “The pristine myth: the landscape of the Americas in 1492”. *Annals of the Association of American Geographers* 82:3, 369-385.

Devall, Bill (1982). “John Muir as deep ecologist”. *Environmental Review* 6:1, 63-86. DOI: 10.2307/3984050

Dewsbury, Donald A. (1995). “Americans in Europe: the role of travel in the spread of European ethology after World War II”. *Animal Behaviour* 49, 1649-1663.

Dugnol, B., C. Fernández, G. Galiano, and J. Velasco (2008). “On a chirplet transform-based method applied to separating and counting wolf howls.” *Signal Processing* 88, 1817–1826.

Dunbar, R. I. M. (2004). “Gossip in evolutionary perspective”. *Review of General Psychology* 8:2, 100-110. DOI: 10.1037/1089-2680.8.2.100

Dunbar, R. I. M. (2017). “Group size, vocal grooming and the origins of language”. *Psychonomic Bulletin & Review* 24, 209–212. DOI 10.3758/s13423-016-1122-6

Durbin, Leon S. (1998). “Individuality of the whistle call of the Asiatic wild dog *Cuon alpinus*”. *Bioacoustics* 9:3, 197-206. DOI: 10.1080/09524622.1998.9753395

Faragó, Tamás, Attila Andics, Viktor Devecseri, Anna Kis, Márta Gácsi and Ádám Miklósi (2014). “Humans rely on the same rules to assess emotional valence and intensity in conspecific and dog vocalizations”. *Biology Letters* 10: 20130926. http://dx.doi.org/10.1098/rsbl.2013.0926

Federal Animal Damage Control Act of 1972: Hearings, Ninety-second Congress (1972). Committee on Commerce. Subcommittee on the Environment. Washington: US Government Printing Office

Filibeck, Umberto, Marcello Nicoli, Patrizia Rossi, and Giorgio Boscagli (1982). “Detection by frequency analyzer of individual wolves howling in a chorus: A preliminary report”. *Italian Journal of Zoology* 49:1-2, 151-154. https://doi.org/10.1080/11250008209439382

Flores, Dan (2016). *Coyote America: A Natural & Supernatural History*. New York: Basic Books, Hachette Book Group.

Frederiksen, J. K. and C. N. Slobodchikoff (2007). “Referential specificity in the alarm calls of the black-tailed prairie dog”. *Ethology Ecology & Evolution* 19:2, 87-99. DOI: 10.1080/08927014.2007.9522569

Gazzola, Andrea, Elisa Avanzinelli, Lorenza Mauri, Massimo Scandura, and Marco Apollonio (2002). “Temporal changes of howling in south European wolf packs”. *Italian Journal of Zoology* 69:2, 157-161. DOI: 10.1080/11250000209356454.

Gipson, Philip (1995). “Wolves and Wolf Literature: A Credibility Gap”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 347-353. Stillwater: Voyageur Press, 1995.

Goodmann, Patricia A., Erich Klinghammer, and Jessica Willard (2002). *Wolf Ethogram*. Eckhard H. Hess Institute of Ethology.

Gould, James L. and Carol Grant Gould (1994). *The Animal Mind.* New York: Scientific American Library.

Gräfe, Sophia and Alexandra Hui (2020). “Temporalizing space through sound and movement: the Günter Tembrock protocols on fox behavior”. *Sound & Science: Digital Histories*, Epistemes of Modern Acoustics research group.

Griffin, Donald R. (2000). “Scientific approaches to animal consciousness”. *American Zoologist* 4, 889–892. https://doi.org/10.1093/icb/40.6.889

Grooms, Steve (2008). “The mixed legacy of *Never Cry Wolf*”. *International Wolf* 18:3, 11-13.

Haber, Gordon and Marybeth Holleman (2013). *Among Wolves: Gordon Haber’s Insights into Alaska’s Most Misunderstood Animal.* Fairbanks: University of Alaska Press.

Hailman, Jack P. and Millicent S. Ficken (1986). “Combinatorial animal communication with computable syntax: Chick-a-dee calling qualifies as ‘Language’ by structural linguistics”. *Animal Behaviour* 34:6, 1899-1901. https://doi.org/10.1016/S0003-3472(86)80279-2

Harrington, Fred H. (1978). “Ravens attracted to wolf howling”. *Condor* 80, 236-237.

Harrington, Fred H. (1987). “Aggressive howling in wolves”. *Animal Behaviour* 35:1, 7-12.

Harrington, Fred H (1989). “Chorus howling by wolves: acoustic structure, pack size, and the Beau Geste effect”. *Bioacoustics* 2:2, 117-136. DOI: 10.1080/09524622.1989.9753122

Harrington, Fred H. and Cheryl S. Asa (2003). “Wolf Communication”. In *Wolves: Behavior, Ecology, and Conservation* ed. L. David Mech and Luigi Boitani, 66-103. Chicago: The University of Chicago Press.

Harrington, Fred H. and L. David Mech (1978). “Wolf howling and its role in territory maintenance”. *Behaviour* 68:3-4, 207-249. DOI: 10.1163/156853979X00322

Harrington, Fred H. and L. David Mech (1982). “An analysis of howling response parameters useful for wolf pack censusing”. *The Journal of Wildlife Management* 46:3, 686-693.

Harrington, Fred H. and L. David Mech (1983). “Wolf pack spacing: Howling as a territory-independent spacing mechanism in a territorial population.” *Behavioral Ecology and Sociobiology* 12, 161-168.

Hauser, Marc D. (1996). *The Evolution of Communication*. Cambridge: The MIT Press.

Hauser, Marc D. and Peter Marler (1993). “Food-associated calls in rhesus macaques (Macaca mulatta): II. Costs and benefits of call production and suppression”. *Behavioral Ecology* 4:3, 206–212. https://doi.org/10.1093/beheco/4.3.206

Hennely, Lauren, Bilal Habib, Holly Root-Gutteridge, Vicente Palacios, and Daniela Passilongo (2017). *Current Zoology* 63:3, 341–348. doi: 10.1093/cz/zox001

Henshaw, Henry W. (1908). “The Policemen of the Air: An Account of the Biological Survey of the Department of Agriculture”. *The National Geographic Magazine* 19, 2.

Hittell, Theodore H. (1861). *The Adventures of James Capen Adams, Mountaineer and Grizzly Bear Hunter, of California.* Boston: Crosby, Nichols, Lee and Company.

Horizons O'er the Musselshell: Detailed portraits of early Musselshell County settlers, families, ranches and schools. (1974). Hougardy, Beulah C., Hazel Spidel, Alice B. Graves, and Frances Spek (eds). Roundup: Musselshell Valley Pioneer Club.

Hornaday, William T. (1914). *Wild Life Conservation in Theory and Practice.* New Haven: Yale University Press.

Howell, A. Brazier (1930). “At the Cross-Roads”. *Journal of Mammalogy* 11:3, 377-389, https://doi.org/10.2307/1374159.

Iron Cloud, Manuel (1995). “Sungmanitu Tanka Oyate: Wolf Nation”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 260-262. Stillwater: Voyageur Press, 1995.

Jaynes, Julian (1969). “The historical origins of ‘ethology’ and ‘comparative psychology’”. *Animal Behaviour* 17, 601-606.

Jones, Helen Carey (1990). *Custer County Area History: As We Recall*. Dallas: Curtis Media Corporation. Montana Historical Society Research Center via Montana Memory Project.

Jones, Karen (2003). “*Never Cry Wolf*: Science, sentiment, and the literary rehabilitation of *Canis lupus*”. *The Canadian Historical Review* 84:1, 65-93, https://doi.org/10.3138/CHR.84.1.65.

Joslin, Paul W. B. (1967). “Movements and home sites of timber wolves in Algonquin Park”. *American Zoologist* 7:2, 279-288.

Kaplan, Jonas T. and Marco Iacoboni (2006). “Getting a grip on other minds: mirror neurons, intention understanding, and cognitive empathy”. *Social Neuroscience* 1:3-4, 175-83. doi: 10.1080/17470910600985605

Kershenbaum, Arik and Marie A. Roch (2013). “An image processing based paradigm for the extraction of tonal sounds in cetacean communications”. *The Journal of the Acoustical Society of America* 134:6, 4435–4445. https://doi.org/10.1121/1.4828821

Kershenbaum, Arik, Holly Root-Gutteridge, Bilal Habib, Janice Koler-Matznick, Brian Mitchell, Vicente Palacios, and Sara Waller (2016). “Disentangling canid howls across multiple species and subspecies: Structure in a complex communication channel”. *Behavioural Processes* 124, 149–157. http://dx.doi.org/10.1016/j.beproc.2016.01.006

Kershenbaum, Arik, Éloïse C. Déaux, Bilal Habib, Brian Mitchell, Vicente Palacios, Holly Root-Gutteridge, and Sara Waller (2017). “Measuring acoustic complexity in continuously varying signals: how complex is a wolf howl?” *Bioacoustics* 27:3, 215-229. DOI: 10.1080/09524622.2017.1317287

Kershenbaum, Arik, Jessica L. Owens, and Sara Waller (2019). “Tracking cryptic animals using acoustic multilateration: A system for long-range wolf detection”. *The Journal of the Acoustical Society of America* 145, 1619. doi: 10.1121/1.5092973

Latour, Bruno (1987). *Science in Action.* Cambridge: Harvard University Press.

Leblond, Mathieu, Christian Dussault, and Martin-Hugues St-Laurent (2017). “Space use by gray wolves (*Canis lupus*) in response to simulated howling: a case study and a call for further investigation”. *Can. J. Zool*. 95, 221–226. dx.doi.org/10.1139/cjz-2016-0191

Leopold, Aldo (1919). “Wild Lifers vs. Game Farmers: A Plea for Democracy in Sport”. *Bulletin of the American Game Protective Association* Vol. 8, 6-7

Leopold, Aldo (1949). *A Sand County Almanac, and Sketches Here and There.* New York: Oxford University Press.

Lopez, Barry (1978). *Of Wolves and Men.* New York: Scribner, 2004.

Lopez, Barry (2020). “Barry Lopez on the wolf biologist who changed his life as an environmentalist: How Bob Stephenson incorporated indigenous knowledge systems in his work”. To appear in *Nunamiullu Amabullu: Nunamiut and Wolves Local Knowledge from the Inland Iñupiat of Northern Alaska* ed. S. Craig Gerlach and James Nageak.

MacNulty, Daniel R, Douglas W. Smith, L. David Mech, John A. Vucetich, and Craig Packer (2012). “Nonlinear effects of group size on the success of wolves hunting elk”. *Behavioural Ecology* 23:1, 75-82. DOI: https://doi.org/10.1093/beheco/arr159

MacNulty, Daniel R., Aimee Tallian, Daniel R. Stahler, and Douglas W. Smith (2014). “Influence of group size on the success of wolves hunting bison”. *PLoS ONE* 9:11. https://doi.org/10.1371/journal.pone.0112884

Manser, Marta B. (2001). “The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency”. *Proceedings of the Royal Society B: Biological Sciences* 268:1483, 2315–2324. doi:10.1098/rspb.2001.1773

Marler, Peter (1970). “Birdsong and speech development: Could there be parallels? There may be basic rules governing vocal learning to which many species conform, including man”. *American Scientist* 58:6, 669-673.

Marshall, Joseph M., III (1992). “The Wolf: A Native American Symbol”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 286-288. Stillwater: Voyageur Press, 1995.

Mazzini, Francesco, Simon W. Townsend, Zsófia Virányi, and Friederike Range (2013). “Wolf howling is mediated by relationship quality rather than underlying emotional stress”. *Current Biology* 23, 1677–1680. http://dx.doi.org/10.1016/j.cub.2013.06.066

McIntyre, R., J. B. Theberge, M. T. Theberge, and D. W. Smith (2017). “Behavioral and ecological implications of seasonal variation in the frequency of daytime howling by Yellowstone wolves”. *Journal of Mammalogy*, 98:3, 827–834. DOI: 10.1093/jmammal/gyx034

McIntyre, Rick (1995). “Hunting Their Lost Tribe”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 15-28. Stillwater: Voyageur Press, 1995.

McIntyre, Rick (2016). Yellowstone Wolf Project Liaison. Notes from conversations in the field, January-April 2016.

Mech, L. David (1966). *The Wolves of Isle Royale.* Fauna of the National Parks of the United States Series #7. Washington, DC: US Government Printing Office.

Mech, L. David (1994). “Buffer zones of territories of gray wolves as regions of intraspecific strife”. *Journal of Mammalogy* 75:1, 199-202.

Mech, L. David and Luigi Boitani (2003). “Wolf Social Ecology”. In *Wolves: Behavior, Ecology, and Conservation* ed. L. David Mech and Luigi Boitani, 1-34. Chicago: The University of Chicago Press.

Mech, L. David and Rolf O. Peterson (2003). “Wolf-Prey Relations”. In *Wolves: Behavior, Ecology, and Conservation* ed. L. David Mech and Luigi Boitani, 131-157. Chicago: The University of Chicago Press.

Melis, A., B. Hare, and M. Tomasello (2006). “Engineering cooperation in chimpanzees: tolerance constraints on cooperation”. *Animal Behavior* 72: 275–286.

Mitchell, Brian R., Maja Makagon, Michael M. Jaeger, and Reginald H. Barrett (2006). “Information content of coyote barks and howls”. *Bioacoustics* 15:3, 289-314. DOI: 10.1080/09524622.2006.9753555.

Morton, Eugene S. (1977). “On the ocurrence and significance of motivation-structural rules in some bird and mammal sounds”. *The American Naturalist* 111:981, 855-869.

Muntz, Erich M. and Brent R. Patterson (2004). “Evidence for the use of vocalization to coordinate the killing of a white-tailed deer, *Odocoileus virginianus*, by coyotes, *Canis latrans*”. *The Canadian Field-Naturalist* 118, 278-280.

Murie, Adolph (1944). *The Wolves of Mount McKinley.* Fauna of the National Parks of the United States Series #5. Seattle: University of Washington Press, 1985.

Nagel, Thomas (1974). “What is it like to be a bat?” *The Philosophical Review* 83:4, 435-450.

Naguib, Marc and R. Haven Wiley (2001). “Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication”. *Animal Behaviour* 62, 825–837
doi:10.1006/anbe.2001.1860

National Park Service (2020). “Wolf Pups Born on Isle Royale”. News Release.

National Park Service, Isle Royale National Park (2018). “Record of Decision: Full Environmental Impact Statement to Address the Presence of Wolves at Isle Royale National Park”. US Department of the Interior.

Nelson, Michael P., John A. Vucetich, Rolf O. Peterson, and Leah M. Vucetich (2010). “The Isle Royale wolf–moose project (1958-present) and the wonder of long-term ecological research”. *Endeavour* 35:1, 30-38. doi:10.1016/j.endeavour.2010.09.002

Niemeyer, Carter (2010). *Wolfer*. Boise: BottleFly Press.

Nixon, Richard (1972). “Special Message to the Congress Outlining the 1972 Environmental Program”. Gerhard Peters and John T. Woolley, The American Presidency Project.

Noad, Michael J., Douglas H. Cato, M. M. Bryden, Micheline-N. Jenner, and K. Curt S. Jenner (2000). “Cultural revolution in whale songs”. *Nature* 408: 537.

Nowak, Sabina, Włodzimierz Jezdrzejewski, Krzysztof Schmidt, Jörn Theuerkauf, Robert W. Mysłajek, and Bogumiła Jezdrzejewska (2007). “Howling activity of free-ranging wolves (Canis lupus) in the Białowieza Primeval Forest and the Western Beskidy Mountains (Poland)”. *Journal of Ethology* 25:3, 231-237.

Olson, Sigurd (1938). “A study in predatory relationship with particular reference to the wolf”. *The Scientific Monthly* 46:4, 323-336.

Palacios, Vicente, Enrique Font, and Rafael Márquez (2007). “Iberian wolf howls: Acoustic structure, individual variation, and a comparison with North American populations”. *Journal of Mammalogy* 88:3, 606-613. https://doi.org/10.1644/06-MAMM-A-151R1.1

Palacios, V., E. Font, R. Márquez, and P. Carazo (2015). “Recognition of familiarity on the basis of howls: a playback experiment in a captive group of wolves”. *Behaviour* 152, 593-614. DOI: 10.1163/1568539X-00003244

Palacios, Vicente, Hosé Vicente López-Bao, Luis Llaneza, Carlos Fernández, and Enrique Font (2016). “Decoding group vocalizations: The acoustic energy distribution of chorus howls is useful to determine wolf reproduction”. *PLoS ONE* 11:5, e0153858. doi:10.1371/journal.pone.0153858

Passilongo, D., A. Buccianti, F. Dessi-Fulgheri, A. Gazzola, M. Zaccaroni, and M. Apollonio (2010). “The acoustic structure of wolf howls in some Eastern Tuscany (Central Italy) free ranging packs”. *Bioacoustics*, 19:3, 159-175. DOI: 10.1080/09524622.2010.9753622.

Passilongo, Daniela, Marianna Marchetto, and Marco Apollonio (2017). “Singing in a wolf chorus: structure and complexity of a multicomponent acoustic behaviour”. *Hystrix Italian Journal of Mammalogy* 28:2, 180-185. doi:10.4404/hystrix-28.2-12019

Payne, Roger S. & Scott McVay (1971). “Songs of Humpback Whales”. *Science* 173:3997, 585-597.

Peters, Roger P. and L. David Mech (1975). “Scent-Marking in Wolves: Radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well”. *American Scientist* 63:6, 628-637.

Peterson, Brenda (1994). "Wolf Medicine". In *War Against the Wolf: America's Campaign to Exterminate the Wolf* ed. Rick McIntyre, 444-461. Stillwater: Voyageur Press, 1995.

Petroelje, Tyler R., Jerrold L. Belant, and Dean E. Beyer, Jr. (2013). "Factors affecting the elicitation of vocal responses from coyotes *Canis latrans*". *Wildlife Biology* 19, 41-47. DOI: 10.2981/12-022.

Phillips, Michael K. and Douglas W. Smith (1997). *Yellowstone Wolf Project Biennial Report 1995 and 1996*. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR- NR-97-4.

Piattelli, Michela (2016). "'Language is our Rubicon': Friedrich Max Müller's quarrel with Hensleigh Wedgwood". *Publications of the English Goethe Society* 82:2-3, 98-109. DOI: 10.1080/09593683.2016.1224511

Pimlott, D. H. (1960). "The use of tape-recorded wolf howls to locate timber wolves". Toronto: 22nd Midwest Fish and Wildlife Conference.

Pinker, Steven (1994). *The Language Instinct: How the Mind Creates Language.* New York: Harper Perennial.

Placer, J. and C.N. Slobodchikoff (2004). "A method for identifying sounds used in the classification of alarm calls". *Behavioural Processes* 67, 87–98. doi:10.1016/j.beproc.2004.03.001

Placer, John, C. N. Slobodchikoff, Jason Burns, Jeffrey Placer, and Ryan Middleton (2006). "Using self-organizing maps to recognize acoustic units associated with information content in animal vocalizations." *The Journal of the Acoustical Society of America* 119:5, 3140-3146.

Pollard, Kimberly A. and Daniel T. Blumstein (2012). "Evolving communicative complexity: insights from rodents and beyond". *Philosophical Transactions of the Royal Society B* 367, 1869–1878. doi:10.1098/rstb.2011.0221

Prather, Jonathan F. and Richard Mooney (2015). "Mirror neurons in the songbird brain: a neural interface for learned vocal communication". In *New Frontiers in Mirror Neurons Research* ed. Pier Francesco Ferrari and Giacomo Rizzolatti. Oxford: Oxford University Press (2015).

Radick, Gregory (2007). *The Simian Tongue: The Long Debate about Animal Language*. Chicago: The University of Chicago Press.

Redington, Paul G. (1928). *Report of Chief of Bureau of Biological Survey.* U.S. Department of Agriculture, Bureau of Biological Survey. Washington: U.S. Government Printing Office.

Reilly, Patrick (2020). “Fish and Wildlife Commission tightens wolf, elk hunting rules”. *Missoulian,* Missoula.

Revise wolf hunting laws, H.B. 73, 63rd Legislature, 2013 Regular Session (MT 2013).

Richards, Douglas G. and R. Haven Wiley (1980). “Reverberations and Amplitude Fluctuations in the Propagation of Sound in a Forest: Implications for Animal Communication”. *The American Naturalist*, 115:3, 381-399. http://www.jstor.org/stable/2460725

Robinson, Michael J. (2005). *Predatory Bureaucracy: The Extermination of Wolves and the Transformation of the West.* Boulder: The University Press of Colorado.

Root-Gutteridge, Holly, Martin Bencsik, Manfred Chebli, Louise K. Gentle, Christopher Terrell-Nield, Alexandra Bourit, and Richard W. Yarnell (2014a). “Improving individual identification in captive Eastern grey wolves (Canis lupus lycaon) using the time course of howl amplitudes”. *Bioacoustics* 23:1, 39-53. DOI: 10.1080/09524622.2013.817318

Root-Gutteridge, Holly, Martin Bencsik, Manfred Chebli, Louise K. Gentle, Christopher Terrell-Nield, Alexandra Bourit, and Richard W. Yarnell (2014b). “Identifying individual wild Eastern grey wolves (*Canis lupus lycaon*) using fundamental frequency and amplitude of howls”. *Bioacoustics* 23:1, 55-66. DOI: 10.1080/09524622.2013.817317

Schenker, Natalie M., William D. Hopkins, Muhammad A. Spocter, Amy R. Garrison, Cheryl D. Stimpson, Joseph M. Erwin, Patrick R. Hof, and Chet C. Sherwood (2010). “Broca's Area Homologue in Chimpanzees (Pan troglodytes): Probabilistic Mapping, Asymmetry, and Comparison to Humans”. *Cerebral Cortex* 20:3, 730-742.

Servín, Jorge (2000). “Duration and frequency of chorus howling of the Mexican wolf (Canis lupus baileyi)”. *Acta Zool. Mex* 80, 223-231.

Seyfarth, R. M., D. L. Cheney, and P. Marler (1980). “Monkey responses to three different alarm calls: evidence of predator classification and semantic communication”. *Science* 210:4471, 801-803. DOI: 10.1126/science.7433999

Seyfarth, Robert M. and Dorothy L. Cheney (2014). “The evolution of language from social cognition”. *Current Opinion in Neurobiology* 28, 5-9. DOI: http://dx.doi.org/10.1016/j.conb.2014.04.003

Shoemaker, Henry W. (1914). *Wolf Days in Pennsylvania*. Altoona: The Tribune Press.

Slobodchikoff, C. N., J. Kiriazis, C. Fischer, and E. Creef (1991). “Semantic information distinguishing individual predators in the alarm calls of Gunnison’s prairie dogs”. *Animal Behaviour* 42:5, 713-719. https://doi.org/10.1016/S0003-3472(05)80117-4

Slobodchikoff, C. N., Andrea Paseka, and Jennifer Verdolin (2009). “Prairie dog alarm calls encode labels about predator colors”. *Animal Cognition* 12:3, 435-9.

Smith, Doug (2019). Senior Wildlife Biologist, Yellowstone National Park. Phone interview, 13 August 2019.

Smith, Doug and Gary Ferguson (2012). *Decade of the Wolf, Revised and Updated: Returning the Wild to Yellowstone*. Guilford: Lyons Press.

Smith, Douglas W., L. David Mech, Mary Meagher, Wendy E. Clark, Rosemary Jaffe, Michael K. Phillips, and John A. Mack (2000). “Wolf-bison interactions in Yellowstone National Park”. *Journal of Mammalogy* 81:4, 1128-1135.

Smith, D.W., D.R. Stahler, K.A. Cassidy, E. Stahler, M. Metz, C. Meyer, J. Rabe, N. Tatton, J. SunderRaj, L. Carroll, M. Jackson, B. Cassidy, and E. Loggers (2020). *Yellowstone Wolf Project Annual Report 2019.* National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2020-01.

Smith, W. John (1977). *The Behavior of Communicating: An Ethological Approach*. Cambridge: Harvard University Press.

Smith, Joshua N., Anne W. Goldizen, Rebecca A. Dunlop, & Michael J. Noad (2008). “Songs of humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions”. *Animal Behaviour* 76, 467-477. DOI: 10.1016/j.anbehav.2008.02.013

Steiner, Rick (2012). “Falling wolf population in Alaska's Denali National Park should concern us all”. *Anchorage Daily News*, Anchorage.

Steinhart, Peter (1995). *The Company of Wolves*. New York: Vintage Books.

Stephenson, Robert O. and Robert T. Ahgook (1975). “The Eskimo Hunter’s View of Wolf Ecology and Behavior”. In *The Wild Canids: Their Systematics, Behavioral Ecology, and Evolution* ed. Michael W. Fox, 286-291. Reprint. Wenatchee: Dogwise Publishing, 2009.

Stiner, Mary (2002). “Carnivory, Coevolution, and the Geographic Spread of the Genus Homo”. *Journal of Archaeological Research* 10:1.

Stuart, Granville (1866-1867). “Forty Years on the Frontier”. In *War Against the Wolf: America’s Campaign to Exterminate the Wolf* ed. Rick McIntyre, 58-60. Stillwater: Voyageur Press, 1995.

Suzuki, Toshitaka N. (2014). “Communication about predator type by a bird using discrete, graded and combinatorial variation in alarm calls.” *Animal Behaviour* 87, 59-65. http://dx.doi.org/10.1016/j.anbehav.2013.10.009.

Tembrock, G. (1963). “Acoustic behavior of mammals”. In *Acoustic Behavior of Animals*, ed. T. G. Busnel. London: Elsevier Publishing Co.

Tembrock, Gunter (1976). “Canid vocalizations”. *Behavioural Processes* 1, 57-75.

Theberge, John (1969). “Observations at a rendezvous site in Algonquin Park”. *The Canadian field-naturalist* 83, 122-128.

Theberge, John and Mary Theberge (2016). “Why Wolves Howl”. *Yellowstone Science* 24:1, 61-64.

Theberge, John B. and J. Bruce Falls (1967). “Howling as a means of communication in timber wolves”. *Am. Zoologist* 7, 331-338.

Theberge, John B. and Mary T. Theberge (1998). *Wolf Country: Eleven Years Tracking the Algonquin Wolves*. Toronto: The Canadian Publishers.

Theuerkauf, Jörn, Włodzimierz Jędrzejewski, Krzysztof Schmidt, Henryk Okarma, Ireneusz Ruczyński, Stanisław Śniezko, and Roman Gula (2003). “Daily patterns and duration of wolf activity in the Białowieza Forest, Poland”. *Journal of Mammalogy* 84:1, 243–253. https://doi.org/10.1644/1545-1542(2003)084<0243:DPADOW>2.0.CO;2.

Thoreau, Henry David (1906). *The Writings of Henry David Thoreau: Journal VIII: November 1, 1855-August 15, 1856,* ed. Bradford Torrey. Boston: Houghton Mifflin and Company.

Tinbergen, N. (1963). “On aims and methods of ethology”. *Zeitschrift für Tierpsychologie* 20, 410-433.

Tomasello, Michael, Alicia P. Melis, Claudio Tennie, Emily Wyman, and Esther Herrmann (2012). “Two Key Steps in the Evolution of Human Cooperation: The Interdependence Hypothesis”. *Current Anthropology* 53:6, 673-692. DOI: https://doi.org/10.1086/668207

Tooze, Z. J., F. H. Harrington, and J. C. Fentress (1990). “Individually distinct vocalizations in timber wolves, *Canis lupus*.” *Animal Behaviour* 40:4, 723-730. DOI:10.1016/S0003-3472(05)80701-8

Tremere, Liisa A., Jin Kwon Jeong, and Raphael Pinaud (2009). “Estradiol Shapes Auditory Processing in the Adult Brain by Regulating Inhibitory Transmission and Plasticity-Associated Gene Expression”. *Journal of Neuroscience* 29:18, 5949-5963. DOI: https://doi.org/10.1523/JNEUROSCI.0774-09.2009

Valencius, Conevery Bolton (2013). *The Lost History of the New Madrid Earthquakes.* Chicago: The University of Chicago Press.

Wacewicz, Slawomir and Przemysław Żywiczyński (2014). "Language Evolution: Why Hockett's Design Features are a Non-Starter". *Biosemiotics* 8:1. DOI: 10.1007/s12304-014-9203-2

Walker, Brett (2005). *The Lost Wolves of Japan.* Seattle: University of Washington Press.

Watson, Stuart K., Simon W. Townsend, and Friederike Range (2018). "Wolf howls encode both sender- and context- specific information". *Animal Behaviour* 145, 59-66. DOI: 10.1016/j.anbehav.2018.09.005

Wedgwood, F. J. (1873). Darwin Correspondence Project, Letter # 8994. https://www.darwinproject.ac.uk/letter/DCP-LETT-8994.xml

Whitney, W. D. (1974). "Darwinism and Language". *The North American Review* 119:244, 61-88.

Wielgus, Robert B. and Kaylie A. Peebles (2014). "Effects of wolf mortality on livestock depredations". *PLoS ONE* 9:12, e113505. https://doi.org/10.1371/journal.pone.0113505

Wilden, I., H. Herzel, G. Peters, and G. Tembrock (1998). "Subharmonics, biphonation, and deterministic chaos in mammal vocalization". *Bioacoustics: The International Journal of Animal Sound and its Recording* 9:3, 171-196. http://dx.doi.org/10.1080/09524622.1998.9753394

Wiley, R. Haven and Douglas G. Richards (1978). "Physical Constraints on Acoustic Communication in the Atmosphere: Implications for the Evolution of Animal Vocalizations". *Behavioral Ecology and Sociobiology*, 3:1, 69-94. http://www.jstor.org/stable/4599157

Wineman, Elva (1930). "Famous White Killer Wolf Lived an Almost Unbelievabel [sic] Career: Canny Monarch of Montana Wilds Evaded Scores of West's Finest Hunters of Years, Carried Price of $400 on His Head". *Democrat News*, Lewistown, MT.

Wilson, E. O. (2012). *The Social Conquest of Earth*. New York: Liveright.

Wilson, Paul J., Sonya Grewal, Ian D. Lawford, Jennifer N. M. Heal, Angela G. Granacki, David Pennock, John B. Theberge, Mary T. Theberge, Dennis R. Voigt, Will Waddell, Robert E. Chambers, Paul C. Paquet, Gloria Goulet, Dean Cluff, and Bradley N. White (2000). "DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a

common evolutionary history independent of the gray wolf". *Canadian Journal of Zoology* 78:12, 2156–2166. https://doi.org/10.1139/z00-158

Wilson, W. E. "Limestone" (1880). "A Buffalo Hunt in the '80's." Lewistown: Lewistown Public Library.

Woodruff, G. and D. Premack (1979). "Intentional communication in the chimpanzee: The development of deception." *Cognition* 7:4, 333–362. doi:10.1016/0010-0277(79)90021-0

Zaccaroni, M., D. Passilongo, A. Buccianti, F. Dessì-Fulgheri, C. Facchini, A. Gazzola, I. Maggini, and M. Apollonio (2012). "Group specific vocal signature in free-ranging wolf packs". *Ethology Ecology & Evolution* 24:4, 322-331. DOI: 10.1080/03949370.2012.664569