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Using Dentition as an Indicator of Senescence in Eurasian Lynx (Lynx lynx) and Wolverines (Gulo gulo)

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Eurasian Lynx (*Lynx lynx*) and Wolverines (*Gulo gulo*)

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Using Dentition as an Indicator of Senescence in Eurasian Lynx (*Lynx lynx*) and Wolverines (*Gulo gulo*)

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ABSTRACT

Senescence is the age-related progressive deterioration of an organism over time upon reaching maturity. While Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*) have been extensively studied in regard to their physical characteristics, behavior, life cycle, and habitat, there is limited data on the damage and wear of their teeth, which are excellent indicators of health and overall condition of an organism. The goal of this study was to identify if senescence in conjunction with foraging strategy is associated with dental deterioration and how these factors could affect quality of life. I worked with the Norwegian Institute for Nature Research in Trondheim, Norway to assess skulls from their laboratory as well as storage unit within the NTNU University Museum for this study. Individuals identifiable by maturity and sex were used resulting in a total of 61 lynx and 44 wolverines studied. Dentition was visually assessed to determine degree of wear and what types of damage were sustained. Lynx, which are obligate carnivores, were found to have virtually no wear on average on their canines and premolars whereas the wolverines, being facultative scavengers, also had little wear on their premolars and molars but their canines were worn to a smooth tip on average. Wolverines exhibited significantly more wear and damage than lynx. Future studies pertaining to the relationship of senescence and dental health could substantiate findings provided they are able to obtain data from not only a large quantity of specimens from a species, but also equal amounts of each sex and variety of ages particularly from early maturity to geriatric status.

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CHAPTER I

INTRODUCTION

1.1 Importance of Study

Dental health affects the overall health of humans (Lee et al. 2009), so it likely affects the overall health of wildlife species as well. Understanding the effects of how and why dental wear and damage occurs and how it can factor in to long-term health among predators is a largely understudied field of research (Wenker et al. 1999). Further investigation into this aspect of life could allow for in-depth interpretations of conservation needs including viable population counts amongst both predators and prey to determine optimum numbers needed to ensure healthy, long-term survival of species. Because predators are so reliant on their teeth to consume their prey, this could be an important part of their fitness and therefore warrants additional study.

Through study of the skeletal system of an organism, it is possible to gain an in-depth look into its life by learning about things such as what kinds of foods it ate, where it lived, and injuries it had sustained. By examining the relationship between damage and degradation processes of this system, we can learn how and why an organism was successful in its environment (Akkus et al. 2003). The gradual deterioration of an organism's body as a result of aging, also known as senescence, is an area of importance when looking at a species with a longer lifespan, especially one that is currently experiencing a decline in its population (Turbill and Ruf 2010; Williams 1957). As described by Gaillard et al. (2004), senescence occurs when an individual has decreased reproductive ability and/or survivability due to advanced age. Teeth, in particular, provide information about an animal's life chemically, microscopically, and macroscopically. The life of an animal is uniquely "written" in their dentition, unlike the rest of the skeletal system, which is protected internally while the teeth encounter the animal's environment directly each day.

1.2 Study Purpose and Objectives

While studies have investigated the relationship between tooth wear and damage and individual age for species around the world, but none has focused on the comparison of species with differing foraging strategies. While foraging strategy is not the sole difference between species, it can be used as an indicator to build upon when addressing the process of senescence amongst them. If we can interpret data to learn about how and why organisms age as they do, we would be able to gain greater understanding of species on an individual level and as a whole, which can contribute to conservation efforts and wildlife management. As of 2010, the Eurasian lynx (*Lynx lynx*) is listed as "vulnerable" and the wolverine (*Gulo gulo*) listed as "endangered" according to the Norwegian Red List (Hanssen 2015), so it is valuable to acknowledge the potential impacts of senescence on these species. Conservation and management strategies of threatened and endangered species of carnivores are frequently treated as though the strategies are separate entities rather than cohesive units which can benefit from looking at ecosystems as a whole (Linnell and Strand 2000; Glen and Dickman 2005). So, this study is not only touching upon the relationship of dentition to age, but taking into account the relationship of carnivores that share the same land and prey to potentially aid in evaluation of such strategies to support their conservation management needs together.

In this thesis, I present the results of my study conducted in Trondheim, Norway through the Norwegian Institute for Nature Research that aimed to identify the relationship, if any, between tooth damage and wear and age among two predator species, Eurasian lynx and wolverines. These species partake in different strategies to obtain their food, one as an obligate carnivorous predator and the other as a facultative scavenger (Mattisson et al. 2011b). How does senescence play a role in tooth wear and damage? Do species with differing foraging strategies differ in the amount of wear and damage in their dentition? By uncovering and comparing these relationships, we can gain a greater insight into the lives of these species, which may be essential in conservation of not only these two species, but those of comparable life histories. The objective of this research was to assess if there is a correlation between age and the amount and type of dental damage sustained among these species. My hypotheses were that lynx would have a lesser average degree of wear and frequency of damage than wolverines and that canines would exhibit the greatest amount of both wear and damage of all tooth types among both lynx and wolverines. The findings of this study could benefit the species by providing awareness into alterations in conservation and management strategies that may be needed to maintain healthy, viable populations even with events such as culling and harvesting that take place in Norway each year. This thesis includes a literature review chapter that explores and synthesizes the research on the potential impacts of dental health due to senescence and a chapter presenting the findings of this study and interpreting its results.

CHAPTER II

THE IMPACT OF DENTAL CONDITION AMONG AGING PREDATORS

2.1 Introduction

In Scandinavia, Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*) have been increasingly intensively studied following their recovery after near extirpation in the mid-20th century (Khalil et al. 2014). The Norwegian government maintains strict control over regulation of population numbers and yearly goals for individuals and family groups to meet management plan goals that allow for viable sustainable populations (Andersen et al. 2003) set forth by the Climate and Environment Ministry, which is the authority that is responsible for all wildlife management in Norway. Despite such regulation, between 2010 and 2018, there have been declines in the lynx population from between 13 and 44% following their peak population count of 92 family groups in 2009. According to Rovdata, an official database linked with the Norwegian Institute for Nature Research (NINA) for monitoring lynx, wolverines, brown bears, wolves, and golden eagles in Norway, the current population of lynx is at a count of 57.5 family groups for the year 2018 with an estimated 340 individuals (Tovmo and Zetterberg 2018). Wolverines experienced a decline of 20% from 2016 to 2017 resulting in a total of 40 family groups and 324 individuals (Eklund et al. 2017). Because of wavering population trends in lynx in Norway and the beginnings of such for wolverines, it is important to look even more closely at the biology of these species to better understand the factors contributing to their survival as well as their intraspecific and interspecific relationships (Abramov et al. 2009; Khalil et al. 2014; Mattisson et al. 2011a).

Unless wild animals are consistently tracked and observed through monitoring systems such as radio-collars and telemetry or camera traps, it is difficult to gain insight into the lives of individuals and populations. While Eurasian lynx and wolverines are two species of predator that NINA frequently studies and monitors (Linnell et al. 2005; May et al. 2008) including research on ecology, population status, management practices, human-wildlife conflicts, predator-prey relationships, and interspecific interactions (Linnell et al. 2005), there is still little to no data on how to interpret rates of senescence, or age-related deterioration of survivorship and/or fecundity among these two species (Williams 1957; Turbill 2010). Biologists are recently appreciating that senescence is complex and can be observed in not only fecundity, but also behavior and physiology (Ericsson et al. 2001; Carranza et al. 2004; Reimers et al. 2005; Angelier et al. 2007).

As stated by Kirkwood and Austad (2000), "As a rule, wild animals simply do not live long enough to grow old." By studying the process by which animals age regardless of whether or not they reach geriatric status, a greater understanding of a species' life history can be gathered to project their long-term health and viability in the wild. Aging is a multifaceted process, which varies by species and affects different areas of life history at varying rates (Jones et al. 2008; Turbill and Ruf 2010). One such area is dentition as senescence is believed to affect teeth through damage and wear over time, which is affected by animal behavior, including foraging strategy. Dentition is a valuable subject of study as it provides an understanding of life history evidence for each individual, which can lead the way to learning more comprehensive information about a species as a whole (Alt 1999). In this literature review, I will address what is known about the relationship between predator foraging and dental deterioration and highlight the fact that this relationship is an understudied area of the wildlife aging process. The purpose of the review is to identify the current knowledge of dental condition with age as well as the gaps that need further inquiry. Through gaining a thorough understanding of how a species ages, we can better address their longevity in the wild and conservation concerns. Looking at the life histories of both lynx and wolverines allows for a background of not only foraging strategy but behavior to build upon to gather a picture of social dynamics that can impact dental wear and damage over a lifetime.

2.2 Life Histories

Understanding a species' life history can provide insights into the aging process of that species. In order to obtain a greater grasp of the senescence process, we must look at how animals live their daily lives to interpret how their longevity can be impacted by the choices they make. Foraging strategy is one such aspect of life that could play a role in the survival, fecundity, and quality of life of individuals.

The Eurasian lynx, henceforth lynx, is the third largest predator in Europe following the brown bear (*Ursus arctos*) and wolf (*Canis lupus*). Lynx are obligate carnivores (Pedersen et al. 1999; Mattisson 2011b), whose major prey in Europe are roe deer (*Capreolus capreolus*), but they can also survive on smaller prey such as hares, grouse, and other small ungulates (Odden et al. 2006), which leads them to also be referred to as opportunistic generalist predators (Jędrzejewski et al. 1996). In both Norway and Sweden in Sámi reindeer husbandry areas, reindeer depredation by lynx is common throughout the year (Pedersen et al. 1999; Sunde et al. 2000). In areas where domestic sheep (*Ovis aries*) are present, lynx have been found to incorporate them into their diets, which may be primarily due to easier accessibility than wild prey (Odden et al. 2006). Wild lynx that survive to adulthood have a lifespan range of typically

2-5 years, but have been noted to live up to 17 years (Nowell and Jackson 1996). As lynx from different regions throughout Norway have access to different prey sources, it is possible that dental maladies differ according to geographic region in addition to age.

Wolverines are the largest terrestrial member of the weasel family (Mustelidae). The wolverine is classified as both a predator and facultative scavenger (Pasitschniak-Arts and Larivière 1995; van Dijk et al. 2008; Mattisson et al. 2011a; Khalil et al. 2014). Prey include a wide array of species such as birds, voles, lemmings, hares, and small ungulates (Pasitschniak-Arts and Larivière 1995). They are dependent on their strong jaws to consume frozen meat and bones. During the winter months, reindeer (*Rangifer tarandus*) is the most important food source (Haglund 1966; Myhre and Myrberget 1975), particularly as carrion (Mattisson et al. 2011a), which they commonly obtain by taking advantage of kills by lynx and wolves. However, snow cover allows for optimal conditions for wolverines to actively hunt ungulates because they are capable of walking atop the snow whilst ungulates do not have the capability (Krott 1959; Pasitschniak-Arts and Larivière 1995). Food caching is another way wolverines retain their food, which is done by keeping food buried in snow, hidden in rocks, watercourses, or swamps in the summer (Pasitschniak-Arts and Larivière 1995; Landa et al. 2000; Inman et al. 2012). Wolverines have a life expectancy of 4-6 years in the wild with a maximum of 13 years (Abramov et al. 2009). Unlike lynx, wolverines are found only found in Norway from about the middle of the country through the far north. Because of this, the prey sources of wolverines will not be likely to include that of sheep, which would be an easier source of prey, which could result in a lesser likelihood of struggle, which could result in dental trauma.

While aging plays an expected role in the survival of an organism, the behaviors of lynx and wolverines, including foraging strategies, are likely to be a major contributing factor to their overall health and longevity in the wild (Galbany et al. 2011). Among both species, high contact behaviors are required for either subduing and/or consuming prey that they either hunt themselves or scavenge (van Dijk et al. 2008; Odden et al. 2006). These behaviors require acts of contact between prey and teeth can result in instances of tooth wear, breakages, or even loss during a single interaction or accumulate over time to cause such afflictions (Galbany et al. 2011). Cumulative damages are to be anticipated given the nature of predators, but a severe break, tooth loss, or even excessive wear on the dental structure could result in a hindrance in ability to obtain prey and effectively gain sustenance (Van Valkenburgh 2009). With age, the accumulated wear and damage of teeth can lead to disadvantages in foraging and, because of that, a reduction in quality of life (Mysterud et al. 2001). The notion that a lessened efficiency for feeding due to a decrease dental quality has been thought to impact the rate of senescence in ungulates (Tyler 1987; Gaillard et al. 1993), so it would be expected that such would also be impactful in the lives of predators as well. However, whether or not the effects of such dental traits amongst predators such as lynx and wolverines result in a higher rate of senescence than among ungulates is unknown. Looking at the composition of teeth, the age of individuals through dental analysis, and evaluating dental wear and damage to assess overall health could provide insight into how to conserve wildlife and understand their lifestyles. While age estimation through dental study is commonly used (Garde et al. 2010; Kryukova 2014), interpretations of the impacts of dental deterioration on quality of life and aging is lacking. This area of study could aid in interpreting the impact of foraging strategy on tooth condition potentially even to the point of specifically noting a relation of prey type to tooth health. In this next section, I address how dental composition, age estimation, and dental degradation are valuable information to compile to wholly encompass the effects of lifestyle with age.

<u>2.3 Dentition</u>

2.3.1 Composition

To understand how aging impacts dental health, it is essential to determine a baseline peak quality of dentition to then be able to quantify losses in quality over time (Galbany et al. 2011). Such baselines have yet to be determined for Eurasian lynx and wolverines to accurately measure their average rate of wear and types of damage. Bones are primarily composed of organics, particularly collagen, minerals (mainly calcium and phosphate), and water (Yan et al. 2007). Teeth are similarly formed mainly of collagen, but also consist of dentin, which is the most abundant mineralized tissue of the teeth (Nalla et al. 2003). The organic matrix of type I collagen in conjunction with proper hydration of the bone are essential to their resilience and toughness (Zioupos et al. 1999; Nyman et al. 2006). There have been few studies to date to provide quantitative data and evaluation of fracture toughness of dentin (Yan et al. 2007). While teeth are resilient and can withstand considerable damage, including cracking, before failing to be used further, they do become susceptible to infection and/or loss when enduring high loads of stress (Maas and Dumone 1999). The maximum stress load and its relation to structural strength must be observed based on both the direction and position of the load to gain a true understanding of the integrity of each tooth type (Freeman and Leman 2006). This study will result in a reference of strength and integrity based on foraging strategy that could be built upon in future studies with quantifiable data to potentially measure stress loads over time in a controlled environment.

Indeed, mammalian teeth can be used as indicators of environmental stress, which can provide insights into the daily and overall interactions that species have had with their environment and how they cope with various wear and damage over time. Addressing the effects of such interactions throughout a lifetime can allow a more detailed understanding of how and why certain behaviors among predators impact why different species may live longer than others or have more stressful lives trying to cope with dental loss which, particularly in carnivores, could result in less successful hunting and inability to properly consume food with age (Dayan et al. 2009). Identifying the age of individuals can be of great use to gauge the process of dental wear and damage over each year, especially upon reaching maturity, among species.

2.3.2 Age Estimation

Methods for determining ages of mammalian wildlife have been developing since the late-1960s. Common methods for carnivores included tooth eruption (Slaughter et al. 1974), crown wear (Harris 1978; Stander 1997; Gipson et al. 2000), pulp chamber closure x-rays (Marks and Erickson 1966; Binder and Van Valkenburgh 2010), and counting of cementum lines through tooth sectioning (Matson 1981). The most effective approach was the process of counting the incremental lines in tooth cement (Harris 1978; Dimmick and Pelton 1996; Klevezal 1996; Nakanishi et al. 2009). While an accurate method for most species, the need for tooth extraction and laboratory analyses generated ethical problems and delays in age determination. A faster, less invasive way to gauge wild animal ages was necessary, which led to the development of mammal studies based on tooth wear (Chevallier et al 2017).

Deterioration of teeth is an important area of study as it is suggested that tooth degradation negatively affects body condition and performance of an individual (Gaillard et al. 1993). According to Wood (1958), tooth wear is considered to be the most indicative criterion for age determination, but Van Valkenburgh (1988) considers tooth breakage and loss to be dependent on age and therefore key indicators of aging as well. If natural selection has resulted in the pressure to retain teeth capable of withstanding normal wear and damage associated with daily life for various species' requirements, teeth should be able to function as needed until death (Van Valkenburgh 1988). However, carnivores have been found to have varying degrees of wear, fracturing, and breakages of their teeth, especially amongst those that consume bone (Van Valkenburgh 1988, 2009). Lynx are reliant on their canine teeth to take their prey through a fatal bite to the throat or back of the neck (Anyonge 1996; Slater and Van Valkenburgh 2009) and do not masticate their meat (Romer 1953), so are not likely to incur severe fracturing and breakage when obtaining and consuming their food, whereas wolverines rely far more on the use of their premolars to consume food. These carnassial teeth are essential to access the nutrients of bones and must be of strong integrity to endure a lifetime of this feeding strategy without resulting in debilitating damage (van Dijk et al. 2008; O'Brien et al. 2014). Because of these dietary needs, carnivores in particular, are dependent on the longevity and durability of teeth, which are of great importance to ensure a good quality life (Aghashani et al. 2016). I will now review the causes of wear and damage in wildlife dentition and how such can greatly impact quality of life with age.

2.3.3 Tooth Degradation

The analysis of microscopic dental wear can provide strong evidence of diet and foraging strategy from days to even months prior to death. These analyses can reflect how carcasses are utilized and dietary preferences (Stynder et al. 2012). While microwear can give more exact data of the effects of foraging strategy, the study of macrowear provides valuable insight that can be more quickly and easily studied especially if working in the field and do not have the time and resources to do such in-depth examinations (Chevallier et al. 2017; Strömquist et al. 2009).

Wear of teeth results from life experiences of individuals including the compounding effects of diet, properties of food, behavior, tooth morphology, and enamel structure (Cuozzo et al. 2010). Abrasion and attrition, tooth-food contact and tooth-tooth contact respectively, are the two primary types of tooth wear, which result in the loss of enamel and dentin over time (Galbany et al. 2014). Consequently, the appearance of teeth will change as age increases and older individuals will display cracks, fractures, wear, defects, among other oral maladies (Carvalho and Lussi 2017). The most common mode in which teeth are affected is the incisors followed by canines, premolars, and molars (Wenker et al. 1999; Cuozzo and Sauther 2006; Strömquist et al. 2009). This pattern is thought to be due to the differences in enamel structure and thickness as well as the presence of dentin (Strömquist et al. 2009). Aside from typical erosion of enamel, facets and caries, which are more commonly known as cavities, may form which may inhibit an individual's capacity to properly obtain and consume food due to an inability to shear and tear meat and/or pain from a dental pathology to render individuals incapable of such activities.

Fractures and breakages typically result from diet and are most commonly present in the canines (Strömquist et al. 2009), especially amongst those species that consume bone. Specialist bone crackers have been found to have stronger mandibles below their canine and premolar regions to allow resistance to high masticatory stress (Kruuk 1973; Biknevicius et al. 1996). Incidences such as these while more common with age and wear, are capable of occurring to varying degrees as a result of a single event as opposed to environmental factors that have resulted in a loss or diminishment of structural integrity (Van Valkenburgh and Fritz 1993; Clough et al. 2010). As tooth enamel is brittle, chipping is not uncommon (Constantino et al. 2010). It has been hypothesized that different tooth forms have adapted to resist fracture to accommodate the needs of a species to obtain, break down, and consume their food (Lawn et al. 2013).

Due to the canine tooth shape and function, they may undergo a greater amount of bending than other teeth (Van Valkenburgh 1988) and may be afflicted with a greater amount of direct contact during times of aggression, which can lead the way to a breakdown of teeth in the form of fracturing and/or breakages (Verstraete et al. 1996). This impact on dentition can also be attributed to mechanical stress loads that the skull shapes in relation to temporal muscle and mandible form of felids and mustelids such as these can handle (Radinsky 1981a; Radinsky 1981b; Radinsky 1982). The mandible is an excellent indicator to understand dietary adaptations (Meloro 2011), so taking an even closer look at the effects of those adaptations can help to understand the toll such strategies take on the dentition that they rely on for survival.

We can assume that the older an animal is, the more wear and damage there is to be identified should no extraneous premature deterioration have occurred such as intraspecific and interspecific behavioral altercations (Strömquist et al. 2009). According to Binder and Van Valkenburgh (2010), tooth damage occurs in accordance with tooth wear, which is primarily a result of a combination of age and foraging strategy. Dental degradation is found to be heavily influenced by how species obtain and consume their prey (Christiansen 2008). It has been hypothesized that damage is affected by not only the foraging strategy and consumption methods of food, but also individual body size, prey size, and intraspecific and interspecific species aggression. However, these factors have been found to be of significantly less impact on damage (Slater and Van Valkenburgh 2009). Felids are all obligate carnivores, which means that they solely consume vertebrate prey (Van Valkenburgh 1988; Slater and Van Valkenburgh 2009), so their probability of tooth wear and damage is likely to be lesser than those species which routinely break and consume bone as a primary source of sustenance. Such carnivorous species, like wolverines, that use their teeth to consume as much of the body of the prey as possible have higher frequencies of fracture and breakages (Van Valkenburgh 1988).

Because mammals have no tooth replacement following the emergence of their secondary permanent set of teeth, premature losses can result in major consequences that threaten the survival of an individual (Cuozzo et al. 2010). Whether by complete loss, which results in ossification of the jaw bone where the tooth once was, or damage, which may result in the resorption of a tooth if broken severely enough, the inability to use canines and carnassial teeth could very well result in an inability to sustain through sustenance and/or protect oneself from opponents. Therefore, there is a selective pressure to maintain the structural integrity of teeth to ensure survival to the point of ensuring fitness in the wild, especially regarding fecundity (Schwartz et al. 2003), while allowing for degrees of loss with age without risking effectiveness in foraging strategy to maintain a good quality of life (Maas and Dumone 1999; Ungar 2010).

2.4 Conclusion

Aging plays a key role in the ecology of individuals, greatly affecting their abilities to survive and reproduce, which, in turn, can result in changes in the demography and dynamics of wildlife populations (Chevallier et al 2017). Of the few studies focusing on mammalian aging processes, most have focused on whether or not senescence is occurring (Gaillard et al. 2004) rather than how it affects a species' survivorship through adulthood. The accumulation of bone damage, especially in that of teeth, can allow an understanding of the relationship of degradation and damage and, therefore, senescence of a species (Akkus et al. 2003). As teeth are excellent indicators of environmental stressors, studying their wear and damage at various ages of adulthood could allow for a deeper understanding of their longevity in the wild in terms of capability to retain physical and reproductive fitness (Badyaev 1998; Klevezal and Sokolov 1999; Dayan et al. 2009). Without dentition including integrity and functionality, the ability to hunt and kill prey is significantly decreased and can affect overall health and lead to the ultimate mortality of an individual (Aghashani et al. 2016). Although wear and damage are associated with age and diet amongst species (Carlsson et al. 1966; Berkovitz and Poole 1977), there have been very few studies that compare tooth wear and damage in relation to foraging strategies.

Evaluating the ages of wild animals based in external tooth condition is a path that can be easily followed for study and built upon over time to determine the effects of dental maladies on a population and its longevity (Binder and Van Valkenburgh 2010). Studies of both extinct and extant species regarding dentition and its correlation to aging are great resources to extrapolate upon to gain a deeper understanding of the effects of lifestyle on physical ability over a lifetime (Ericsson et al. 2001). Knowing how foraging strategy implicates survival through dental integrity would allow for a more thorough comprehension of a given species needs when they are in need of protection and conservation efforts must be put forth for their retention in the wild (Loison et al. 2001). Should a species such as the lynx or wolverine need conservation measures aid to protect their populations and long-term viability, this knowledge would allow conservationists to determine what optimal numbers their population should be, including by sex, given the options of prey and the determined general age of longevity for individuals (Bunnefeld et al. 2006).

CHAPTER III

RELATIONSHIP BETWEEN TOOTH WEAR AND DAMAGE AND THE FEEDING STRATEGIES OF TWO CARNIVORES

3.1 Introduction

Among mesopredators such as lynx and wolverines, high contact with prey is essential, which is a result of their particular foraging strategies. Survival and fitness are determinant on the success of hunting (Pyke et al. 1977; Sunde and Kvam 1997; Melville et al. 2004). Interactions with prey pose risks of injury particularly to the teeth of predators and scavengers as they are dependent on accurately subduing prey without causing undo harm to their teeth. Natural selection favors optimizing nutrient intake while minimizing the risk to the predator and the energy they need to expend (Krebs and Davies 1993). Over time, interactions with prey compound to affect the dental structure and integrity of an organism.

Upon reaching maturity, an individual is increasingly subject to the process of senescence with each passing year. Because teeth are not capable of regenerating following any form of wear or damage, wildlife are susceptible to severe impacts on quality of life should extreme wear or major tooth damage or loss occur, especially depending on the type of tooth affected. Those individuals that are near the end of their life expectancy would display such wear and damage to a greater degree than those younger and that have just reached maturity. Since lynx and wolverines have average lifespans in the wild of just 2-5 years for lynx and 4-6 years in wolverines, it may be difficult to interpret data on tooth observations to the point of its effect on senescence as these animals would only been considered mature from 2-3 years of age.

In this study, I aimed to evaluate the relationship between tooth wear and damage and individual age to determine if senescence is a potential mechanism for dentition degradation in two species: the Eurasian lynx and wolverine. These two species were selected because they are highly regulated and primary causes of livestock depredation in Norway (Tveraa et al. 2014). Conservation management for both species could be better influenced and guided with better understanding of the relationship between individual age and physiological factor of tooth condition that could lead to behaviors that cause destruction of property including reindeer and sheep. These species partake in different strategies to obtain their food, one as an obligate predator and the other as a facultative scavenger respectively (Mattisson et al. 2011b). How does senescence play a role in tooth wear and damage? How can foraging strategy indicate the survivorship of a species in the wild in terms of dentition? By uncovering and comparing these relationships, we can gain greater insight into the lives of these species, which may be essential in conservation of not only these two species, but those species with comparable life histories. I conducted this study through the Norwegian Institute for Nature Research using specimens from deceased lynx and wolverines to measure, evaluate, and analyze the wear and damage of the teeth among both species to aim to identify potential relationships between dental wear and damage with regard to age as well as to determine if foraging strategy would result in higher rates of degradation of tooth quality over time. My hypotheses were: 1) Lynx will exhibit less wear and less frequency of damage than wolverines and 2) Canines will exhibit the greatest amount of both wear and damage of all tooth types among both lynx and wolverines.

3.2 Methods

3.2.1 Study Area

This study was conducted in Trondheim, Norway at the Norwegian Institute for Nature (NINA) headquarters laboratory and the Norwegian University of Science and Technology (NTNU) University Museum.

3.2.2 Materials

The skulls used for this study were provided from storage units at the NINA laboratory and the NTNU University Museum. Specimens used from the NINA laboratory, which were not cleaned of tissue, were kept in a freezer in individual bags and were thawed to allow ability to separate the jaws and were dated between 2006 and 2009 for lynx and between 1997 and 2011 for wolverines. Skulls at the museum were previously cleaned and kept in a secured room in individual cardboard boxes with plastic covers and were dated between 1976 and 1986 for lynx and between 1962 and 1986 for wolverines. Specimens had been collected from quota hunting periods by donation from hunters and accidental (e.g. vehicular collisions) and natural deaths, which were obtained through notification to the institute or government by the researchers, government officials, or the general public. Lynx specimens were collected from the Norwegian counties of Troms, Nordland, Nord-Trøndelag, Sør-Trøndelag, Oppland, Hedmark, and Akershus. Wolverine specimens were obtained from the counties Finnmark, Troms, Nordland, Møre og Romsdal, and Hedmark.

A total of 61 lynx skulls (27 male, 34 female) and 44 wolverine skulls (27 male, 17 female) were used. All samples used were adults. The museum specimens each had an enclosed tag, which identified whether the individual was considered to be an adult, juvenile, or unknown. Skulls from the laboratory were not marked, so I had to use my judgment based on my experience from studying the museum skulls to determine visually if the individuals were adults or juveniles. Those specimens that were not identifiable as either adult or juvenile with certainty were not used. Skulls that contained at least half of the individual's dentition were used from the museum and laboratory.

All teeth were measured from the gum line to the tip of the tooth using Biltema digital calipers (Art. 16-105). For skulls that were not cleaned prior to study, scalpels and knives available in the NINA laboratory were used to gain access to the specimens' teeth. Because the skulls in the laboratory were not cleaned, but rather previously skinned, cooked, frozen, and then thawed for study, plastic gloves, laboratory goggles, a laboratory coat, and surgical masks were used.

For each specimen, I recorded the following data: species, NINA identification number, NTNU museum identification number, sex, year obtained, location (most specific area, municipality, county), number of teeth present, presence of supernumery teeth, location of supernumery teeth, and tooth identification markers (presence, loss ante-mortem or post-mortem, evidence of ossification, degree of wear, damage, height).

3.2.3 Tooth Condition Assessment

The *Lynx* genus has a dental formula of I3/3, C1/1, P2/2, M1/1 totaling to 28 teeth (Gomerčić et al. 2009, Elbroch 2006), while the *Gulo* genus has a dental formula of I3/3, C1/1, P4/4, M1/2, which totals to 38 teeth (Elbroch 2006). Data were only collected from adult specimens of each species because juvenile specimens have not yet reached maturity, and therefore are not a factor when considering inquiries concerning senescence. Maturity was accounted for based on size comparison of identified adults. If a specimen was not definitively full-grown, then it was disregarded for study. For each specimen sampled, the presence or absence of each tooth was recorded. If a tooth was absent, a record was taken of whether there it was lost pre- or post-mortem, presence of ossification as indicated by spongy bone where a tooth would have been, and any damage visible on a macroscopic level (Van Valkenburgh 2009). Damage was assessed based on macroscopic evidence as conducted by Strömquist et al. (2009) in which notes regarding the presence of chips, linear fractures, and caries, commonly known as cavities, were recorded. Height and wear was noted for the canines and premolars of lynx and wolverines for both upper and lower jaws. Additionally, height and wear was recorded for the first molars of the lower jaw for wolverines. Measurements for tooth height were recorded to the nearest hundredth of a millimeter using digital calipers from the highest point on each tooth to the base of the crown (Gomeričić 2010). Macrowear of the teeth was organized into categories following those described by Pinto-Llona (2013). These categories which take into account severity of wear were scored between 1 and 9: (1) cusp with unworn cusp tip, (2) cusp with loss of cusp tip, rough topography (3) cusp with loss of cusp tip, smooth topography, (4) cusp affected by rough wear, no facets, (5) cusp affected by smooth wear, no facets, (6) cusp that has facets, (7) cusp with enamel loss and concave dentine wear, (8) presence of carnassial facet, and (9) punctual pre-mortem enamel fractures.

3.2.4 Data Analysis

To assess trends in the data, I took into account species, number of teeth present, and tooth wear and damage to understand how the changes in dentition care associated with foraging strategy for the Eurasian lynx and wolverine senescence. I compared the number of teeth present as well as average tooth wear scores, types of damage sustained, and average percentage of teeth damaged by tooth type between species. To evaluate whether the species exhibited different amounts of wear, I first calculated the average wear score for each individual by averaging the macrowear scores (ranging from 1-9 as described above) for all teeth present for that individual. I then conducted a Wilcoxon rank-sum test to determine whether these average wear scores were different between the species. To assess if the amount of tooth damage differed between species, I conducted Pearson's chi-squared tests for each type of damage (breakages, fractures, chipping, caries, and faceting) by comparing the number of teeth exhibiting that type of damage to the number without that respective type of damage for each species. The null hypotheses for analyses were that there were that there is no relationship between species and wear score nor between species and each type of damage. Sex of the specimens was not considered in the analysis due to a lack of adequate sample size for statistical purposes particularly amongst the lynx samples.

3.3 Results

A total of 105 specimens, 61 lynx and 44 wolverines, were used sampled and included in the analysis this study. There were 27 male and 34 female lynx specimens and 27 male and 17 female wolverine specimens.

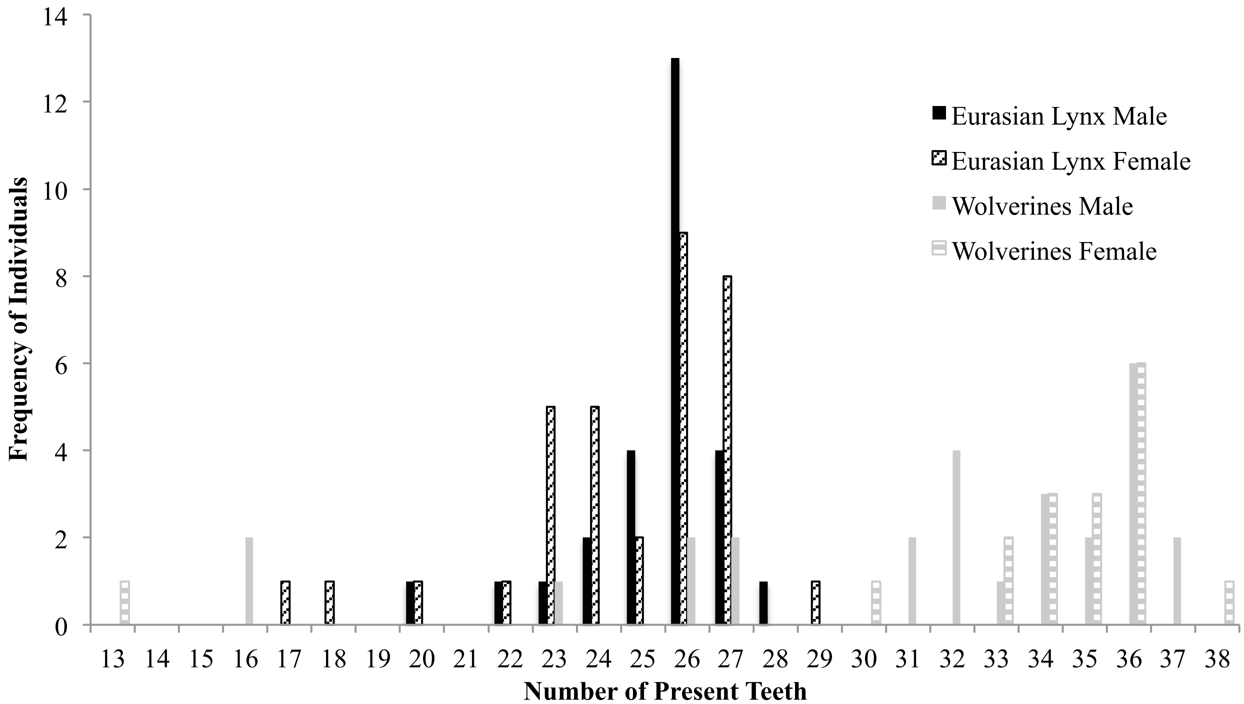

Figure 1. Distribution of number of teeth per specimen sampled of Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) specimens from NINA and NTNU, Norway.

Among studied lynx specimens, both males and females most commonly had 26 teeth present of the expected 28 teeth in their dental formula (Figure 1). Twice as many females as males were found to have 27 teeth. Only one male was found to have a full set of 28 teeth and an outlier female was observed to have 29 teeth, which is a result of a supernumery tooth. Wolverines of both sexes most commonly exhibited the same greatest 36 teeth present of the anticipated 38 according to their dental formula (Figure 1). Only 1 male was found to have 37 teeth and 1 female with a full set of 38 teeth present.

Table 1

Average tooth wear score in Eurasian lynx (Lynx lynx) and wolverine (Gulo gulo) specimens from NINA and NTNU, Norway.

Tooth Type	Eurasian Lynx			Wolverine		
	Average	Standard Deviation	Correlation Interval	Average	Standard Deviation	Correlation Interval
Canines	1.12	0.49	0.26	2.75	1.53	0.32
Premolars	1.03	0.18	0.26	1.41	0.66	0.30
Molars	-	-	-	1.24	1.11	0.32

The degree of wear was determined by the ranking system based on that of Pinto-Llona (2013) that ranges from 1 being the least amount of damage to 9 being the greatest amount sustained before tooth loss occurs. Lynx exhibited an average degree of wear score of 1, which means that the cusp of the tip of each tooth type was unworn. The standard deviation among each tooth type (1^{st} through 4^{th} premolars) was low with only the canine teeth showing a wider variation of wear score with the highest score of 2 (Table 1). Wolverines were found to have an average degree of wear ranging from about 1 to 3 among all tooth types (Table 1). The most worn tooth type were the canines with an average score of nearly 3 with a range possible from 1 to 5.

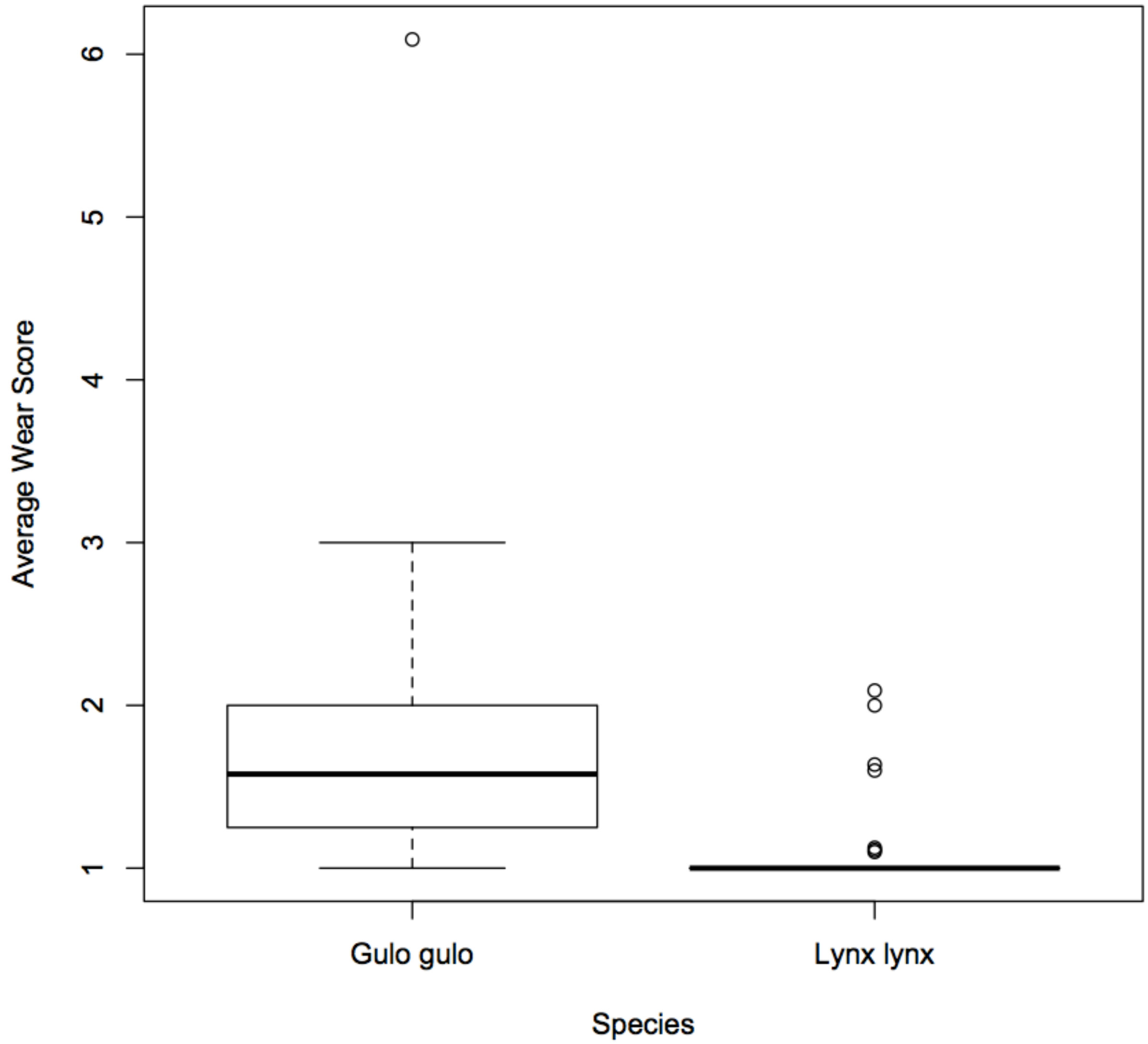

Figure 2. Average tooth wear scores for Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) specimens from NINA and NTNU, Norway.

Results from the Wilcoxon rank-sum test revealed that there is a significant difference between degree of wear between both species (W = 2537.5, p-value <2.2e-16), with wolverines exhibit more wear than lynx (Figure 5). The average wear score for wolverine teeth was 1.75 whereas the average wear score for lynx was 1.06. Wolverines had a wider variation of scoring ranging from 1 to 6 while lynx had just a range from 1 to 2.09.

Table 2

Types of damage accumulated and frequencies of resorption and ossification in each tooth type in Eurasian lynx (Lynx lynx) specimens from NINA and NTNU, Norway.

Tooth Type	Type of Damage					Resorption	Ossification
	Broken	Fractured	Chipped	Caried	Faceted		
Incisors	5	0	2	0	0	0	23
Canines	2	0	1	0	0	0	0
Premolars	6	2	2	1	0	0	2
Molars	2	0	1	1	0	0	0
TOTAL	15	2	6	2	0	0	25

Breaks were the most common form of damage, which were most prevalent among premolars followed by incisors (Table 2). Fracturing occurred only within the premolars. Chipping was evident in each tooth type, but more so among the incisors and premolars. Caries were observed in single instances in both premolar and molar tooth types. Faceting and resorption were not observed. Ossification was found to have occurred primarily among the incisors, but also less so among premolars.

Table 3

Types of damage accumulated and frequencies of resorption and ossification in each tooth type in wolverine (Gulo gulo) specimens from NINA and NTNU, Norway.

Tooth Type	Type of Damage					Resorption	Ossification
	Broken	Fractured	Chipped	Caried	Faceted		
Incisors	12	60	29	7	3	23	42
Canines	18	34	22	7	10	5	1
Premolars	10	349	50	8	1	11	36
Molars	6	86	15	3	1	0	2
TOTAL	46	529	116	23	15	39	81

Each type of damage was also recorded for all tooth types among male and female wolverine specimens. Fracturing was the most common type of damage sustained occurring mostly amongst premolars (Table 3). All other types of teeth had been observed to have high instances of fracturing compared to other types of damage. The frequency of damage type was found to be next highest among chips, breaks, caries, and then facets. Resorption was seen to have occurred in incisors, canines, and premolars. Ossification was most commonly observed in the incisors and premolars with one instance among canines and two among molars.

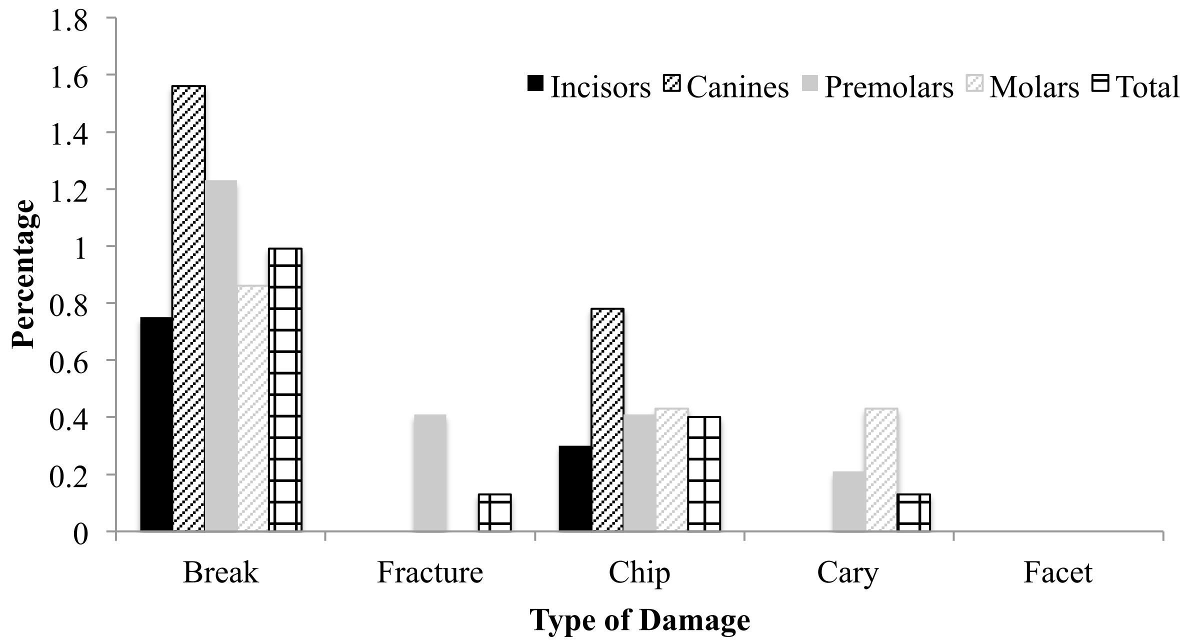

Figure 3. Percentage of present teeth damaged by tooth type in Eurasian lynx (*Lynx lynx*) specimens from NINA and NTNU, Norway.

The percentage of each tooth type containing each type of damage was calculated (Figure 2). The greatest amount of damage was observed in the canines with 1.56% of those teeth broken and 0.78% chipped. Following in increasing rate of damage was the premolars, molars, and then incisors. The greatest instances of breakages occurred among canines (1.56%), fractures among premolars (0.41%), chips among canines (0.78%), and caries among molars (0.43%). Considering all teeth, breaks and chips were most common types of damage at 0.99% and 0.40% respectively followed by an equal amount of overall damage among premolars and molars. Facets were not observed in any tooth type for lynx.

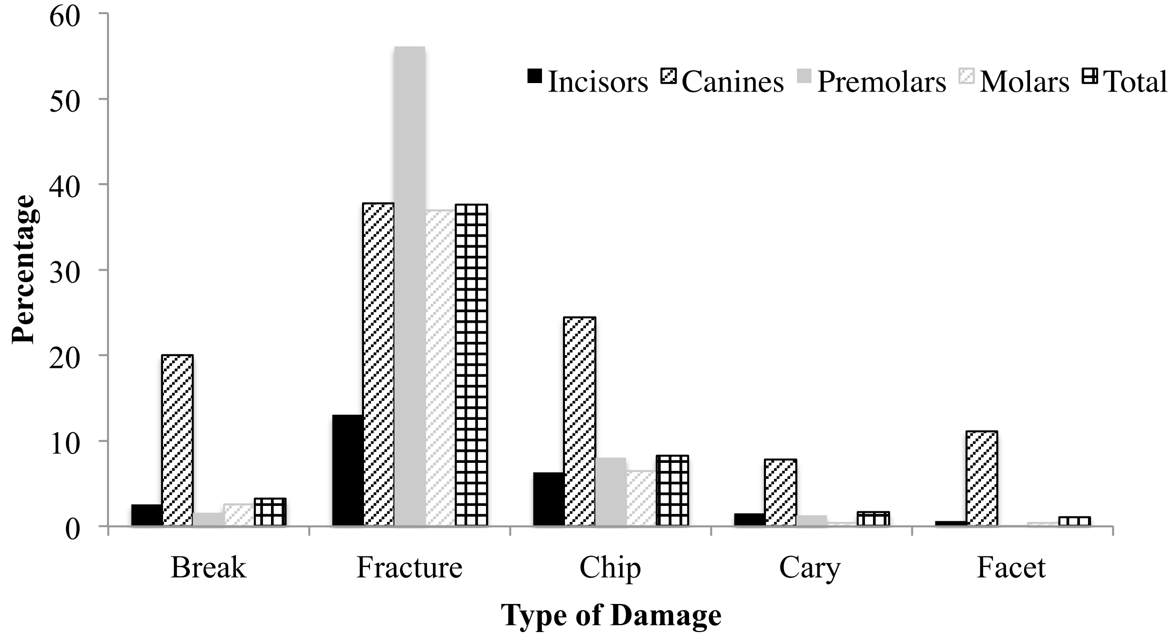

Figure 4. Percentage of present teeth damaged by tooth type in wolverine (*Gulo gulo*) specimens from NINA and NTNU, Norway.

Each tooth type that was found present for all wolverine specimens was assessed and the percentage of each of those tooth types containing each type of damage was calculated. All tooth types were observed to have sustained damage of all types that were studied (Figure 3). The canines displayed the most damage overall of all forms having 20% to nearly 40% either broken, fractured, or chipped with also having nearly 8% of teeth caried and 11% faceted. Across all types of teeth, damage most frequently occurred in the canines followed by premolars, molars, and then incisors. The greatest number of fractures was observed in the premolars having 56.11% of those teeth fractured.

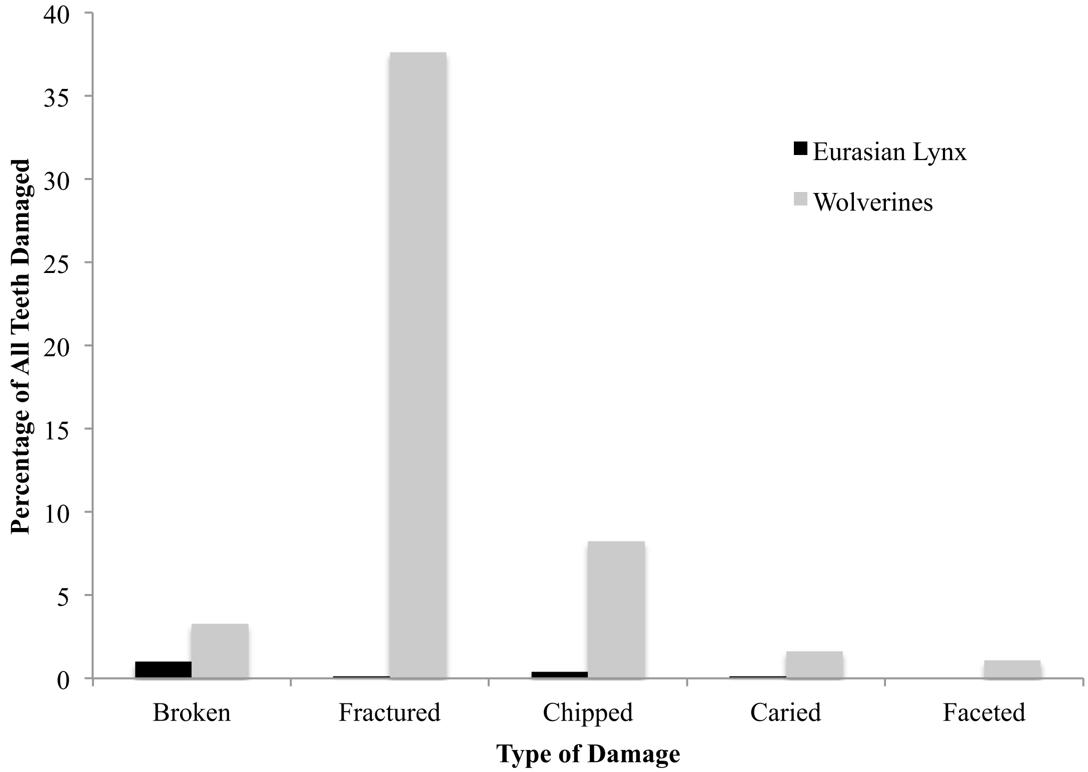

Figure 5. Percentage of all damaged teeth among Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) specimens from NINA and NTNU, Norway.

Wolverines exhibited a greater percentage of damage amongst all types studied (Figure 4). Damage for wolverine dentition ranged from 1.07% for facets, 1.64% for caries, 3.27% for breaks, 8.25% for chips, to 37.62% for fractures. Lynx exhibited 0% damage due to facets, 0.13% for both caries and fractures, 0.40% for chips, and 0.99% for breaks.

Table 4

Percentage of damaged and undamaged teeth and Pearson's chi-squared test results for each type of damage between Eurasian lynx (Lynx lynx) and wolverine (Gulo gulo) specimens from NINA and NTNU, Norway.

Type of Damage	Percentage of Damaged Teeth		Percentage of Undamaged Teeth		Pearson's chi-squared *p*-value
	Lynx	Wolverines	Lynx	Wolverines	
Broken	0.99%	3.27%	99.01%	96.73%	1.74e-05
Fractured	0.13%	37.62%	99.87%	62.38%	<2.2e-16
Chipped	0.38%	8.25%	99.62%	91.75%	<2.2e-16
Caried	0.13%	1.64%	99.87%	98.36%	1.08e-05
Faceted	0.00%	1.07%	100.00%	98.93%	5.72e-05

Wolverines exhibited significantly more damage than lynx in all areas and all types of damage showed statistically significant differences between the two species (breaks: $\chi^2 = 18.45$, d.f. = 1, $p = 1.74e\text{-}05$; fractures: $\chi^2 = 687.14$, d.f. = 1, $p = < 2.2e\text{-}16$; chips: $\chi^2 = 112.00$, d.f. = 1, $p = < 2.2e\text{-}16$; caries: $\chi^2 = 19.36$, d.f. = 1, $p = 1.08e\text{-}05$; facets: $\chi^2 = 16.19$, d.f. = 1, $p = 5.72e\text{-}05$) (Table 4).

3.4 Discussion

As felids are not likely to suffer from great wear and dental fracturing due to their feeding strategy (Slater and Van Valkenburgh 2009; Romer 1953), the results showing that lynx tend to undergo hardly any wear and minimal damage to all teeth were expected. Because wolverines frequently consume bone, the expectation that their teeth would show a greater amount of high degrees of wear and frequency of damage of all types damage than lynx. This was shown by the data in this study and indicates that despite their foraging needs, wolverines do not possess dental composition that has been selected to withstand the exceptional forces that they must endure. These results coincide with the findings from Van Valkenburgh (2009) that tooth fracture is positively correlated to degree of tooth wear. The results thus show us, while ages were not available, that over time the feeding strategy of wolverines as opposed that of lynx could result in a reduction in quality of life and survival should individuals live to older ages than average because of the increased amount of tooth degradation.

The presence of a full set of teeth was found only in one male lynx and one female wolverine studied. The most common number of teeth lost was two resulting in a total of 26 teeth for 13 males and nine females of lynx and 36 teeth for six males and six females of wolverines. These losses result in a 7% reduction in number of teeth for lynx and 5% for wolverines. Given that nearly half of the males and a little over a quarter of the female lynx specimens (36% in total of all lynx specimens) versus 22% of male and 35% of female wolverines (30 in total of all wolverine specimens) lost that same number of teeth was an interesting finding that was not in my expectations. Although lynx suffered fewer dental problems than wolverines, they are still at risk for tooth loss that could eventually be life-threatening. The possibility of wolverines having a stronger mandible and muscular structure to retain teeth despite such harsh foraging strategies could be give reason to why they are less likely to lose teeth even when they are highly worn and damaged (Radinsky 1982).

Wolverines averaged a wear of nearly a 3 in the ranking scale and up to 5 in their canines while lynx averaged about a 1 and up to a 2, suggesting that wolverines truly are more harsh on their teeth than lynx and appear to be more likely to wear and/or break them down at a much faster rate than lynx given their foraging strategy. Tooth wear amongst all premolars regardless of size comparison was distinctly greater amongst wolverines was higher than that of lynx and had larger deviations that lynx premolars had shown. The distinctions between wear between each species suggests that a higher degree of wear is commonly prevalent amongst wolverines than lynx and that could very well lead to problems particularly during hunting times as worn down teeth are not as efficient at penetrating prey and shearing meat (Skogland 1988).

Other forms of dental damage and jawbone reformation in the form of resorption and ossification were not common in the teeth sampled in this study for both species. Caries, or cavities, and facets were nearly non-existent in lynx and rarely present in wolverines. Due to feeding strategies, the presence of such types of damage were likely due to pulling and chewing motions which were especially negatively affecting the incisors as they are so small. The lack of occurrence of such incidences amongst lynx was not surprising as they are a less aggressive species. Because of this, the likelihood of lynx incurring a frequent amount of dental trauma or such severe trauma to result in a significant break or partial or total tooth loss causing either tooth resorption or complete ossification. Wolverines, however, are a much more aggressive species (Persson et al. 2003) with different dietary requirements, which can lead to more frequent incidences of resorption and ossification.

Statistical significances were found to be present for amount of wear between lynx and wolverines as well as among each type of damage. These results show that we can reject the null hypotheses that there is no significant difference in wear or frequency of damage between both species. Wolverines have been found to suffer a greater prevalence of severity of wear and frequency of all types of damage, particularly instances of fracturing, than lynx. These results show that my hypothesis that lynx would exhibit less wear and damage than wolverines is true. However, while my hypothesis regarding canines exhibiting the most wear and damage among both species was correct considering wear and most types of damage, premolars did show a greater percentage of fracturing damage among both species than canines. I found a relationship between the number of teeth present and the number of such that are fractures, and knowing that wolverines suffer fracturing at a high prevalence gives way to question how they are able to fracture so often and yet not only retain their teeth but also how they are still able to effectively use them when their teeth are in such fragile states.

During this study, there were several limitations that inhibited the ability to collect data that would provide more conclusive information on the trends of wear and damage among lynx and wolverines. With the hindrance of ability to obtain the ages of the sampled Eurasian lynx and wolverines, the data gathered was still able to be used for analysis in order address degree of wear and types of damage sustained. This information is still valuable to determine the durability and longevity of teeth, even by tooth type, for these species with regard to their respective foraging strategies. Given the timeframe of my study, the number of specimens able to be measured and studied was restricted. The majority of skulls for both lynx and wolverines were from the 1970s and 1980s. These skulls had been cleaned and chemically treated to remain within the museum, so there is potential for fractures to have been only more evident or even occurred post-mortem due to the drying process as opposed to those newer skulls from the 2000s which had not undergone such processes. Additionally, missing teeth with no signs of ossification and/or resorption were likely due to improper handling which could cause teeth to come loose and become lost over years of study and through changes in storage units, and this probably caused a slight skew in the number of teeth present and, therefore, the study of their wear and damage. Missing canines were most common as usually an upper canine would be taken to determine age and were frequently not matched back with the skull from which they came. As most of the specimens studied were obtained because of quota hunting, additional damage on teeth from attempts to escape from traps could have resulted in more evidence of damage that what might overestimate tooth damage that is truly related to foraging strategy. Additional factors that could have resulted in tooth breaks and fractures other than due to foraging strategy include: significant falls, vehicular collisions, direct blows from an encounter with another animal or object, repetitive forces, and lack of dental density caused by improper nutrition.

For future studies in this area of research, I suggest ensuring that all ages of skulls studied be determined to confirm that the individuals are in fact in the target age range for proper evaluation. If possible, obtaining a larger sample size than what I had available would be ideal to truly see where trends may be in tooth wear and damage with regard to species, sex, region, habitat, and/or prey options. Having larger sample sizes that also contain ages from early maturity to geriatric status, however, is understandably difficult to come by. Due to this, it may be beneficial to have studies such as this conducted every few years with any new available specimens to compile on the previous knowledge to not only evaluate what the newest samples are indicating, but also what the population of a given species is trending to show over time.

This field is one that can built upon over time and provide a great insight into trends of populations, which is invaluable data in terms of conservation management.

CHAPTER IV

CONCLUSION

Both lynx and wolverines have approximately the same typical lifespan in the wild averaging about five years (Nowell and Jackson 1996; Abramov et al. 2009), so the trends in effects and evidence of senescence on tooth wear and damage are difficult to observe and analyze. However, the data collected from this study were still able to give indications of common dental problems that each species are more likely to endure and compound over time to eventually cause stressors to the quality of life of an individual. Across both wear and all types of damage, lynx were clearly and remarkably resilient to the effects of their foraging strategies on their dentition with the average wear being as little as possible past the point of perfect dental formation and a grand total of 1.65% of all 1,510 teeth studied affected by any form of damage. Meanwhile, wolverines exhibited a higher degree of wear in all quantified tooth areas and had 51.85% of 1,406 teeth studied impacted by any type of damage studied. Evidently, the lifestyle of wolverines is making a profound impact on the quality of their teeth while lynx are able to also be effective predators without high risk to their dental integrity. This begs the question of if wolverines and lynx numbers were no longer strictly maintained by the government to allow for some aging individuals to persist, would wolverines naturally die off sooner than lynx because their teeth could not endure a long lifetime of a foraging strategy with high instances of bone-crushing? Foraging strategy may be an indicator of the quality of teeth over time with regard to structural integrity and usefulness and could be a great resource for study to gauge just what impacts on quality of life and lifespan in wildlife species it has in those regards.

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