The Dire Consequences of Specializing on Large Herbivores: A Comparison of Extinct *Canis dirus* and Extant *Canis lupus*

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Abstract

Niche differentiation is a way in which similar species avoid competition. Some species do this by specializing in certain prey items. This review aims to determine why the dire wolf (*Canis dirus*) went extinct while its similar and less abundant relative, the grey wolf (*Canis lupus*) did not. Both species were present in North America during the Pleistocene, though only one went extinct during the Quaternary extinction event. Physiological differences existed between the two species, mostly due to a greater focus in hypercarnivory for dire wolves. Dire wolves had more robust frame and skull, greater bite strength, and larger carnasials and canines. These differences in dire wolf morphology all help it to handle and kill larger prey species, while the more lithe grey wolf is better adapted to switching to smaller alternative prey. Dire wolves at have been shown to consume mostly large herbivores while grey wolves can survive with lagomorphs as a primary food source. Larger carnivore body size means reduction in locomotor performance, which means that when many mega-herbivores went extinct at the end of the Pleistocene, dire wolves were not as well adapted to switch to smaller prey as grey wolves are. Their naturally larger body mass also means that they needed higher caloric input to maintain their body condition and fecundity. Overall, *Canis dirus* specialized in larger prey than *Canis lupus*, so when this prey became extinct, the dire wolf went extinct along with other hypercarnivores such as the North American lion, Smilodon, and short-faced bear.

Keywords: dire wolf, grey wolf, Canidae, extinct, niche specialization, Pleistocene

Introduction

Ecological niche can be thought of as a species' responses to biotic and abiotic factors in their environment which affect survival, growth, or reproduction (Hutchinson 1957). Factors that influence niche include food, temperature, precipitation, days of light, etc. Therefore, ecological niche can be described as a range of environmental conditions in which the species can survive (Smith *et al*. 2014). These adaptations to certain conditions may mean that species become less able to survive in alternate conditions (Smith *et al*. 2014). Niches of similar species differ in order to reduce competition, so that competitive exclusion, the elimination of one species by a superior competitor, does not occur (Hutchinson 1957; Hardin 1960; Smith *et al*. 2014). Instead of species living in their fundamental niche, the full ecological niche of the species, species will instead be restricted to their realized niche, a limited niche which restricts competition with similar species while still allowing

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the species to survive (Hutchinson 1957; Connell 1961; Arakaki & Tokeshi 2011).

Throughout Earth's history, as many as 99.9% of all species that ever existed have gone extinct (Russell *et al.* 2016). As environments change, an average of 10% of poorly adapted species goes extinct every million years (Raup 1986; Russell *et al.* 2016). How one species survives while another similar species does not has been an important area of study in Paleobiology. Minute differences between species can lead to a competitive advantage, resulting in one species surviving while another does not. Specialization is known to elevate the risk of extinction (Van Valkenburgh *et al*. 2004). However, when a specialist niche is available to exploit an unused resource, specialists readily evolve (Van Valkenburgh 2007). This means that for two seemingly similar species, something as small as dietary niche can differ between them so that complete competition does not occur.

The order Carnivora is at least 60 million years old, with caniforms and feliforms branching early in the order's history (Van Valkenburgh 2007). Family Canidae is a distinct branch of the order Carnivora that is more generalized in morphology and ecology than members of Felidae (Goswami 2006). Canids range in size from lone predators and invertivores to hypercarnivores, carnivores that take prey at least 45% their own mass to prey greatly exceeding their body size (Van Valkenburgh & Koepfli 1993; Goswami 2006). The wolf-ecomorph hypercarnivores are known to have broader snouts, greater mechanical advantage for biting, deeper jaws, enlarged canines and incisors, and reduced grinding and greater sheering capacity of molars compared to non-hypercarnivore canids (Van Valkenburgh & Koepfli 1993; Van Valkenburgh 2007; Tedford *et al.* 2009). This ecomorph is considered a generalized hypercarnivore in comparison to members of Felidae or osteophagous specialists like members of Hyaenidae because it has evolved independently in 5 families of Carnivora (Van Valkenburgh 2007). Both *Canis dirus* and *Canis lupus* fit into this hypercarnivore niche.

The dire wolf was a large Pleistocene member of Canidae which can be found at over 100 archaeological sites across North and South America (Kurten & Anderson 1980; Kurten 1984; Stock & Harris 1992; Dundas 1999; Tedford *et al*. 2009). *Canis dirus* likely evolved from *Canis armbrusteri,* which existed in North America over 1 million years ago (Tedford *et al*. 2009). Dire wolves ranged in North America from Alberta to Mexico, with findings in three South American locations, indicating it radiated south as the continents connected (Dundas 1999; Hodnett *et al.* 2009). *Canis dirus* lived in a variety of habitats, from grasslands of the mammoth steppe to forested mountains (Dundas 1999). Most is known about dire wolves from their extensive fossil evidence left at Rancho La Brea, the largest deposit of North American Pleistocene remains, and other mid-latitude locations in North America. Grey wolves evolved in Eurasia, with the earliest recorded appearance in the Middle Pleistocene, about 0.5-0.3 Ma. (Bonifay 1971; Sotnikova 2010). Grey wolves came to the mid-latitude ranges of North America during the late Rancholabrean, 100 thousand years ago, via the Bering land bridge (Tedford *et al*. 2009; Sotnikova 2010). Mostly similarities exist between the two *Canis* species, despite evolving on different continents. Both were hypercarnivores, species specializing in large prey, which hunted in packs. Like grey wolves, dire wolves show low levels of sexual dimorphism in the canines, indicating that they had a pair-bonded breeding structure like that of modern wolves (Van Valkenburgh & Sacco 2002). While much was the same between these two species, enough differences existed that the dire wolf went extinct at the end of the Pleistocene epoch.

The focus of this paper was to examine the niches of two species in the family Canidae. Looking at how these niches differed between similar species will help inform on how one species went extinct, while another species survived. The study focused on the dire wolf (*Canis dirus*) and the grey wolf (*Canis lupus*), two similar hypercarnivores that had ultimately different fates.

Physiological differences

While the dire wolf is similar in size, research has found that they are considerably more heavily built than Pleistocene and extant grey wolf (Nowak 1979; Kurten & Anderson 1980; Anyonge & Roman 2006). The heads of *Canis dirus* have been shown to be more robust and able to withstand greater trauma (Binder et al. 2002). Nowak (1979) found that some Pleistocene grey wolf skulls were unusually small compared with contemporary and modern wolves, possibly indicating character displacement, the altering of one species in response to another, in regions where its range overlapped with the larger dire wolf (Brown & Wilson 1956; Anyonge & Roman 2006). Compared to modern *Canis lupus*, the dire wolf has been suggested to be between 8 and 15% heavier (Stock & Harris 1992; Kurten & Anderson 1980). Anyonge & Roman (2006) estimated dire wolf body mass based on equations relating body mass to cross-sectional geometric properties and linear dimensions of the femur of living members of Canidae. Using these parameters, average masses were found and compared to extant species. The western dire wolf (*C. dirus guildayi*) had a mean mass of 60 kg and the eastern dire wolf (*C. dirus dirus*) averaged 68 kg (Anyonge & Roman 2006). The western dire wolf was, on average, 25% heavier than extant grey wolf, with the eastern dire wolf being 15% heavier than the western subspecies found in Rancho La Brea (Anyonge & Roman 2006). This is heavier than the grey wolf, which ranges from 12 kg to 80kg, with a mean of 40 kg (Mech 1970; Mech 1974; Macdonald 1984). While deemed to be heavier than modern grey wolf, western dire wolves have relatively shorter limbs (Stock and Lance 1948 as found in Anyonge & Roman 2006). Overall, *Canis dirus'* increased body mass and shorter limbs indicate the dire wolf had a stockier build than the slimmer grey wolf with which it coexisted.

Having evolved in separate locations and now overlapping in range, it is difficult to determine whether Allen's rule, that species in colder climates have relatively shorter limbs, or Bergmann's rule, that species within a clade in colder environments grow larger, apply to the difference between these species (Bergmann 1847; Allen 1877). While it could be possible that Allen's and Bergmann's rules do apply between these species as an explanation why dire wolves are more robust than grey wolves, no such study has been conducted. The species evolved in separate locations (Eurasia and North America) and from different ancestors. The climatic conditions of either region at similar timescales have not been compared. After the grey wolf migrated to North America, its geological range overlapped with the dire wolf (Tedford *et al*. 2009). Prothero et al. (2012) found that glacial and interglacial periods during the Pleistocene, which resulted in dramatic changes to climate and habitat, had no statistical effect on the morphology of dire wolves, showing that Allen's and Bergmann's rules did not apply to this species. Yet Bergmann's rule has been shown to apply to modern grey wolves in North America (OKeefe 2013). Overall, it is impossible to tell in this review paper what may have caused the physiological differences between the species over evolutionary time.

While the jaw and craniofacial morphology is similar, there are slight differences between the two species. Overall morphology of the teeth is similar in both species (Merriam 1912; Anyonge and Baker 2006). The morphology of dire wolves and grey wolves only differs at four out of 15 measured indices of cranial measurements and jaw musculature attachments (Anyonge and Baker 2006). Significant differences were found in dentition. Upper dentition of the dire wolf has larger dimensions than in grey wolves (Merriam 1912). *Canis dirus* had larger upper carnassial (P4) with larger blades and the M1 of the lower dentition was also found to be greater in size (Anyonge and Baker 2006). Together, the increased carnassial size suggests a greater shearing and slicing ability (Merriam 1912; Kurten & Anderson 1980; Anyonge and Baker 2006). Lastly, the dire wolf also had slightly larger anterior lower premolars (Anyonge and Baker 2006).

The last difference between the morphology of these wolf species is the moment arm of the temporalis (MAT). The MAT is derived by measuring from the midpoint of mandibular condyle to the apex of the coronoid process and dividing by the dentary length (Anyonge and Baker 2006). *Canis lupus* has a larger MAT, meaning it has greater mechanical leverage of temporalis muscle at the mid mandibular teeth than *Canis dirus* (Anyonge and Baker 2006). However, the dire wolf had significantly wider zygomatic arches and relatively longer temporal fossa, meaning that they had a larger temporalis muscle (Anyonge and Baker 2006). Dire wolves also had a larger backward projection of the inion (Anyonge and Baker 2006). All of this suggests that, despite having less mechanical advantage, the dire wolf had greater bite strength. Wroe *et al.* (2005) measured the bite force quotient (BFQ) of extinct and extant predators using the dry skull method to give estimates based on mechanical advantage and muscle size. *Canis lupus lupus*, the Eurasian subspecies of wolf, has a BFQ of 136, while *Canis dirus* had a BFQ of 163 (Wroe *et al.* 2005). Throughout species, Wroe *et al*. (2005) found that skull width was the best indicator of jaw strength. It then makes sense that the wider jawed dire wolf would have increased bite strength.

Some have suggested that this increased bite strength is an adaptation for habitual bone crushing like the extant spotted hyaena (*Crocuta crocuta*) and extinct *Borphagus secundus* (Kurten & Anderson 1980; Van Valkenburgh & Ruff 1987; Biknevicius & Ruff 1992; Biknevicius & Van Valkenburgh 1996; Meehan & Martin 2003). Evidence for this includes tooth wear in specimens from Rancho La Brea suggestive of bone gnawing (Hill 1991; Van Valkenburgh & Hertel 1993). Also, dire wolf specimens show thickening of the mandible in the carnassial and postcarnassial molars, which indicates propensity for bone crushing (Biknevicius & Van Valkenvurgh 1996). This is also found in extant wolves that participate in bone crushing (Biknevicius & Van Valkenvurgh 1996). Hill (1991), on the other hand, argued that dire wolves lacked specific craniodental adaptations of scavenging bone crushers like the spotted hyaena and *Borphagus secundus*. For example, the canines in *Canis dirus* have been shown to have greater bending strength than other canids, which is useful in the delivery of killing bites to prey (Van Valkenburgh & Ruff 1987). Therefore, it is unlikely that the dire wolf lived a scavenging lifestyle where bone crushing was necessary but was merely better able to crush bone than extant canids. Crushing larger bones is advantageous so the nutritious marrow can be accessed (Biknevicius & Van Valkenvurgh 1996). This indicates that the dire wolf most likely lived a predatory lifestyle like the extant grey wolf (Anyonge and Baker 2006). The major difference was that the dire wolf had a significantly stronger bite and larger canines and shearing teeth than the grey wolf.

Effects of larger size: Prey

It is generally believed that dire wolves were a large wolf species that preferred large prey (Merriam 1912; Kurten & Anderson 1980; Kurten 1984; Stock and Harris 1992; Van Valkenburgh & Koepfli 1993; Van Valkenburgh &

Hertel 1998). Van Valkenburgh and Koepfli (1993) and Van Valkenburgh and Hertel (1998) estimated that prey of 100-300 kg was typical for dire wolves, with prey of 300-600 kg being the largest it was likely to hunt. Anyonge & Roman (2006) argued that the maximum range was probable because the former studies estimated the average dire wolf mass at 50 kg instead of the 60 to 68 kg that their study found. Skeletal injuries also indicate that the dire wolf preferred large prey. Brown *et al.* (2017) studied dire wolf injuries from Rancho La Brea specimens to analyze occurrence of injuries during hunting. They found injuries were evenly spread across all limbs and the whole skeleton, without any areas of concentration (Brown *et al.* 2017). Limb injuries made up 65% of dire wolf traumatic injuries (Brown *et al.* 2017). The cranium and dentary were infrequently injured, but the first three cervical vertebrae were often injured, presumably from neck strains induced from biting large straining prey (Brown *et al.* 2017). Tooth breakage levels and cranial morphology also show that dire wolves were eating larger prey (Binder *et al*. 2002). Overall, injury evidence showed that *Canis dirus* was a pursuit predator like the extant grey wolf, which caught and killed its prey only using its jaws (Brown *et al.* 2017). This injury evidence aligns with a study of modern grey wolves and coyotes, where significantly higher rates of injury occurred in the grey wolves which hunt larger prey (Wobeser 1992).

Bite force estimates and isotope analysis also show that *Canis dirus* preferred large prey. Wroe *et al.* (2005) showed that all hypercarnivores have high bite force quotient. Recall, *Canis dirus* had a greater BFQ than *Canis lupuslupus* showing its favouring of larger prey than grey wolves hunt (Wroe *et al.* 2005). Much like the grey wolf, dire wolves were social hunters who coordinated to take down prey larger than themselves (Wroe *et al.* 2005). Alternatively, isolation hunters are shown to have considerably lower BFQ, meaning they are restricted to smaller prey (Wroe *et al.* 2005). Fox-Dobbs *et al*. (2007) used carbon and nitrogen isotope analysis to analyze the diets of modern grey wolves in two locations to compare to La Brea specimens. Isotope analysis from La Brea shows dire wolves were non-specialist hypercarnivores who consumed all of the abundant megafauna in North America (Fox-Dobbs *et al*. 2007). The Carnivore-specific values show that horse made up 41-69% of the dire wolf diet, while giant sloth (3-25%), mastodon (7-21%), bison (1-13%) and camel (1-13%) made up the rest of the diet in nearly equal proportions (Fox-Dobbs et al. 2007). This shows that large prey, such as mastodons (which could weigh over seven tonnes) and bison, were also hunted by dire wolves, making Anyonge & Roman (2006) correct in their assumption of larger typical prey size (Larramendi 2016). While it is more likely that young mastodons were hunted than mature ones, adult bison, which are in the upper estimated prey mass range, could have been hunted by dire wolf packs since modern wolf packs are able to hunt adult bison (MacNulty *et al*. 2014). It has also been shown that dire wolves scavenged for beached marine mammals and fed on smaller prey species when food was scarce or to supplement its diet (Fox-Dobbs *et al*. 2003).

Extant grey wolves regularly feed on prey from as large as moose (*Alces alces*) to as small as beaver (*Castor canadensis*), arctic hares (*Lepus arcticus*), and lemmings (*Dicrostonyx groenlandicus*) (Fox-Dobbs et al. 2007; Mech 2007; Dalerum et al. 2018). Fox-Dobbs *et al*.'s (2007) isotope analysis results for the diets of modern grey wolves differ by location. On Isle Royale, moose made up 90% of wolf diet by mass, with 85% of moose consumed less than one year old (Fox-Dobbs et al. 2007). Beaver made up the rest of the diet, with hares not making a significant fraction (Fox-Dobbs et al. 2007). In Minnesota, wolves had a range of terrestrial prey, with no dominant prey species (Fox-Dobbs et al. 2007). Szepanski *et al*. (1999) did a similar study of Alaskan wolves, finding that coastal wolves had a range of terrestrial and marine prey while wolves in the interior of Alaska mainly preyed on caribou and moose. Dalerum et al. (2018) studied the diet of arctic wolves (*Canis lupus arctos*) at their most northern ranges in Nunavut and Greenland, showing arctic hares and muskoxen (*Ovibos moschatus*) are their primary food sources. They suggested that wolves can survive in the absence of ungulates if hare and lemming are present since it was the primary food source in all study regions and found in 100% of scat samples for Washington Land wolves (Dalerum et al. 2018). *Canis lupus* can supplement and possibly survive on smaller prey species, where there is no evidence to suggest *Canis dirus* did. Studies have shown that modern wolves prefer large prey such as moose, caribou, and bison, over smaller prey species such as deer, hares, mountain goat, and bighorns (Murie 1944; Stebbler 1944; Cowan 1947; Mech 1966; MacNulty *et al*. 2009). Indeed, packs of wolves are known to routinely kill adult moose weighing up to 500 kg (Mech 1966). This is likely due to the greater food reward for large prey compared to the amount of smaller game that would need to be captured to make up this mass. In all, while both species are known to consume large prey, only the grey wolf is known to survive on smaller prey species.

Effects of larger size: Costs and benefits

Since meat has higher energy content and ease of digestion than plants and arthropods, carnivory is favoured evolutionarily (Van Valkenburgh 2007) but also carries associated risks and impacts. Carnivory leads to higher basal metabolic rates, faster growth rates, and higher fecundity (Van Valkenburgh 2007). Hypercarnivores also evolve rapidly when the niche is available (Van Valkenburgh 2007). At the same time, large carnivore size comes at the increased risk of extinction due to a large body size that needs greater inputs of calories along with the risks associated with being at the highest trophic level (Van Valkenburgh *et al*. 2004). As predators evolve to have advantages against large prey, exchanges occur whereby generalist features are lost (Van Valkenburgh 2007). Examples of this in canids include loss of molars, reduction of grinding areas, larger canines and incisors, shortening of the snout, broadening of the jaw, greater relative bite strength at the canines, and enlargement of carnassials in order to slice meat more efficiently (Van Valkenburgh & Koepfli 1993; Van Valkenburgh 2007).

In Yellowstone National Park, MacNulty *et al*. (2009) measured the grey wolf ability to hunt elk based on three parameters: selecting, attacking, and killing. Ability to select prey, which is based on a burst of speed to single out an elk, was unrelated to body mass for wolves over 39 kg (MacNulty *et al*. 2009). The presumption is that until accelerating muscles were fully developed, increasing mass improved selecting ability, but after, speed was not gained with increasing muscle mass (MacNulty *et al*. 2009). Ability to attack and kill both increased with size, meaning that net success for hunting elk was greatest with the largest wolves (MacNulty *et al*. 2009). Attacking ability was only marginally improved by size, which may just be that larger wolves are less intimidated by their larger prey (MacNulty *et al*. 2009). The grappling techniques required for killing were deemed both muscular and mass based, where a gain in mass, whether muscular or not, would help when handling large prey (MacNulty *et al*. 2009). Overall, this would mean that larger predators are better able to overcome the defences of large prey (MacNulty *et al*. 2009). While large wolves were more adapted for grappling large elk, they were more limited in their locomotor tasks, meaning that they are worse hunters for species that are more difficult to pursue than to handle (MacNulty *et al*. 2009). This indicates that larger wolves are less able to survive in the absence of large prey, because they are less adapted to hunt smaller prey species (MacNulty *et al*. 2009).

The hunting of larger game comes at a cost, where more injuries occur for canids that hunt big game than those that hunt smaller game (Brown et al. 2017). Dire wolf specimens show more bruises than their grey wolf contemporaries (Binder et al. 2002). Grey wolves that hunt bison are known to have the highest injury rate (MacNulty *et al*. 2014). Also, larger pack sizes are needed to take large game (MacNulty *et al*. 2014). Large packs can only be sustained by abundant prey, as has been shown in the moose-wolf relationship (Messier 1994). This means that any decline in the abundance of large prey would have direct impacts on dire wolf populations.

An effect of increasing predator size means that there are higher energy requirements. This results in a necessity to feed on large prey, meaning dire wolves could probably only sustain their large body size by mostly hunting large prey (Carbone *et al.* 1999; 2007; Fox-Dobbs *et al*. 2003). Larger members of Canidae also have larger reproductive investments that mean a trade-off between size and energetic investment to reproduce (Geffen *et al.* 1996). Generally, large canids have more precocial young, resulting in requiring more postpartum care from their social groups (Geffen *et al.* 1996). Therefore, larger predators need to consume large prey using pack hunting techniques in order to maintain their body size and provide nourishment for the raising of their young.

Conclusions

Specialization in large prey, which has a greater energy reward than smaller prey, brings about physiological changes in canids. While larger size has been shown to correlate to success when hunting large prey, it limits the predator's ability to pursue more agile prey species. Large prey also leads to the risk of more injuries. A large body size has higher caloric requirements to maintain mass, locomotion, and to reproduce, so a larger body means a commitment to larger prey.

Overall, many interacting factors likely caused the extinction of the dire wolf. Loss of larger prey, specialized dietary niche, increased susceptibility to injury from hunting, decreased ability to switch to smaller prey, and increased reproductive costs are some of the disadvantages dire wolf had compared to extant grey wolf. It has been shown that *Canis dirus* was a more robust wolf species that mostly consumed large prey. Any dietary specialization increases the risk of species extinction (Van Valkenburgh *et al.* 2004). Large canids are associated with areas where prey is abundant, meaning a decline in prey abundance likely leads to extinction (Geffen *et al.* 2006). Extinction of large North American carnivores likely occurred due to the mega-herbivore extinction of the late Pleistocene, where loss of large prey caused the extinction of large specialist predators which were unable to switch to smaller and faster prey (Van Valkenvourgh & Hertel 1993; 1998; Van Valkenburgh *et al.* 2004). Van Valkenburgh and Hertel (1998) estimated that carnivores of the Pleistocene were more likely to go extinct if they were strictly carnivorous and their dominant prey were over 300 kg in size. The more robust nature of *Canis dirus* would have hindered its ability to catch smaller prey. As shown in modern studies of grey wolves, larger grey wolves have decreased locomotor performance (MacNulty *et al*. 2009). This can be extended to dire wolves. Their more robust bodies would be even more limited in locomotor abilities than that of large but more gracile grey wolves. Therefore, switching to smaller prey was even more difficult for a species more specialized in large prey. Their large body sizes also mean increased metabolic rate, so dire wolves would require greater amounts of food to stay alive and reproduce than grey wolves. Overall, it is not surprising that the dire wolf went extinct. It was specialized on large prey that went extinct or became less abundant, was more robust than grey wolves, so less able to switch to smaller game, yet needed greater caloric input to survive and reproduce.

Grey wolves, like many of the less specialized carnivores that survived into the modern era, can survive on smaller, faster prey. Arctic wolf populations can potentially survive on a hare and lemming diet, while other wolf populations survive on mainly *Odocoileus spp.* (Murie 1944; Stebbler 1944; Cowan 1947; Mech 1970; 2007; Dalerum et al. 2018). These are much smaller and faster prey than what made up the dire wolf diet. This ability to survive on smaller prey is likely due to their less specialized hunting of large prey. Their more gracile forms allow them to better pursue agile prey than their more robust relatives. They also range in sizes much more than the dire wolf, with wolves as small as 12 kg, meaning much less food is required to maintain body health and fecundity (Mech 1970; Mech 1974; Macdonald 1984; Geffen *et al.* 1996; Carbone *et al.* 1999; 2007). Grey wolves were rare and less abundant during the Pleistocene compared to other carnivores (Meachen 2014). Some grey wolves whose range overlapped with dire wolves were smaller than modern grey wolves, possibly due to character displacement, where the larger dire wolves held the larger carnivore niche, so grey wolves grew smaller in response (Brown & Wilson 1956; Nowak 1979; Anyonge & Roman 2006). Only when the other hypercarnivores went extinct that the grey wolf began to flourish and dominate the hypercarnivory role in North America (Meachen 2014). In doing so, it ousted the coyote (*Canis* latrans) from pack hunting carnivory, which it did to a much greater extent during the Pleistocene, to the lone omnivore it is today (Meachen 2014). While the grey wolf was less able to compete with other hypercarnivores during a time of mega-herbivore abundance, it was better able to survive their demise by switching to smaller prey. It then became the most common and successful apex predator in North America, outlasting species like the North American lion, Smilodon, short-faced bear, and its own cousin species, the dire wolf.

Why, in an ever-changing world where habitat and niche are highly dynamic, would specialist species evolve? Dietary specialization is known to elevate the risk of extinction (Van Valkenburgh *et al*. 2004). Van Valkenburgh (2007) stated that hypercarnivores evolve rapidly when the niche of large herbivore predators is available. This is at a cost as large carnivore size means increased extinction risk due to the need for greater input of calories (Van Valkenburgh *et al*. 2004). I think that specialists, such as hypercarnivores, evolve when niches are vacant. The presence of many large prey species means that predators would do well to access some of this food. Since increasing size and specializing in large prey occurs relatively easily, many large carnivores appear from different families They were all able to survive for the Pleistocene epoch, which is relatively long on a species scale. Dire wolves existed for over 100, 000 years. They utilized an available niche which would have been vacant if not for species such as the dire wolf. While specialist species are less able to survive changes in climate, new specialists are likely to evolve during the next climatic epoch in order to fill new niches which did not exist or were left vacant. This means that specialist species are continually likely to evolve since the costs and benefits of specialization must be proportional to those for generalists.

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