

Comparison of *Vulpes lagopus* and *Vulpes vulpes* Skulls from Sympatric and
Allopatric Populations

by

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ABSTRACT

Vulpes vulpes, the red fox, and *Vulpes lagopus*, the arctic fox, have tumultuous taxonomic histories. *V. vulpes* boasts cosmopolitan distribution, in part due to artificial introduction. In all areas, its specialization as a generalist allows it to adapt and thrive. The origins of the North American populations were contested. While recent studies proved the species is a long-term native, the valid name for these foxes is still under discussion. *V. lagopus* recently settled into *Vulpes* – previously, this derived fox resided in its own genus. While DNA indicates *V. lagopus* belongs in *Vulpes*, the phenotypes of reds and arctics are strikingly different. However, in parts of Alaska, these two species live sympatrically, in competition. *V. vulpes* tends to usurp *V. lagopus*. A recent study of tooth morphology revealed greater conservation of dental form in red foxes sharing their ranges with arctics, while another study established general trends in each species' skull dimensions. This study compares the skull shape of both species in sympatric and allopatric populations using 2D morphometrics, focusing on four regions of the skull. I investigate whether or not *V. vulpes* is stabilizing its skull shape in sympatric populations, and if this form is suited to a particular diet.

INTRODUCTION

Vulpes lagopus, the arctic fox, and *Vulpes vulpes*, the red fox, are two of the animal kingdom's most recognizable members. The brightly pelted red fox is ubiquitous in the Northern Hemisphere, found everywhere from meadows to cities to deserts, while the snow-white arctic fox stands alongside the polar bear and the penguins as a cold environment icon. *V. vulpes* is lanky and large for a fox, while *V. lagopus*' build is robust, but also compact and rounded. *V. vulpes*' secret to success is its ability to adapt to new situations. *V. lagopus*, on the other hand, has evolved to fill just one niche. In Alaska, despite its lack of cold weather specializations, *V. vulpes* threatens to oust *V. lagopus* from this niche. The key to the red fox's success may be in its incredible plasticity, and the arctic fox's downfall in its lack thereof. Variable *V. vulpes* in Alaska may be evolving to replace the arctic fox as the region's small canid through adjusting its diet and cold tolerance, while *V. lagopus* may be powerless to prevent the larger interloper's progress due to its smaller size and less adaptable nature.

Skull Plasticity: The Key to Reynard's Success?

Skull shape informs us to many aspects of an animal's lifestyle, including its size and diet. Minute differences between teeth or the shape of bones can be all that differentiates one species from the next, especially fossil taxa, such as horses,⁸⁸ known mainly from dental specimens (Simpson 1943). To track

diversity of cranial form is to trace the paths taxa took evolving to fit one niche and then the next, and yet, while the skull of the African elephant *Loxodonta africana* scarcely resembles that of a *Baleana* whale, a *Typhlops* snake, or the bustard, *Ardeotis kori*, many homologous bones are shared between them. All tetrapod skulls evolved from the same set of ancestral bones (Liem et al. 2001). The incredible differences between them are possible due to the way the skull develops.

Like all parts of the body, no single bone in the skull develops in isolation. The position and development of other tissues, including other nearby, bones, determines the final shape of any given bone, and the structures which govern one bone are in turn governed by each other. The details of complex structures are built not by single and dedicated genes for every curve, but by genes which inform development broadly. Structures are refined by overlapping regions of expression. Regions which respond to change as one, referred to as morphometric growth fields, are capable of producing nuanced, striking shifts in shape and require only simple changes to their developmental process to do so. The giant panda, *Ailuropoda melanoleuca*, was made a classic example of a beast built by growth fields by their champion, D. Dwight Davis. To cope with its nutrient-poor diet of tough bamboo stems, the panda uses a skull built for powerful masticating abilities. The posterior half, where muscular attachments for chewing reside, is wide and robust, and its molars are remarkably rugose on their grinding surface.

Together, the burly skull, bulging muscles, and grating teeth grind tough stalks down. Davis proved this remarkable adaptation was the result of simply widening the head of a basic bear, and indeed, panda-like molars are sometimes seen in particularly broad-headed black bears (Davis 1964). To create change like this, development only has to alter the duration of growth in a given direction continues. Small variations in skull shape are found in every population. Given enough selective pressure, an adaptive shape which originates in minor variation can evolve to an extreme form, and non-adaptive shape can arise as a consequence of following the growth pattern responsible for the adaptive phenotype (Davis 1964).

Two basic alterations in development exploited by canids are paedomorphosis and paramorphosis. Paedomorphosis, retention of juvenile characteristics in an adult form, is achieved by ceasing a character's development early (hypomorphosis), starting it late (post-displacement), or slowing its progress (deceleration). In canid skulls, this presents as a rounded, stubby, sometimes weaker skull, which, like a puppy's, can have a pronounced forehead. Paramorphosis, on the other hand, produces elongated, sometimes stronger, more complex features, such as long snouts and large sagittal crests. Paramorphic features develop beyond the degree they did in ancestral adults by accelerating their development (acceleration), starting it sooner (pre-displacement), or allowing it to carry on longer (hypermorphosis) (Liem et al. 2001).

While selection on basic genetic variation is quite involved in evolution, it can be slow. Processes exist which allow animals able to exploit them to adapt more rapidly. One of these, the Waddington's genetic assimilation, is the process by which a feature normally developed due to exposure to environmental factors over time is switched to one present at birth, or at least sooner in life. This occurs when the presence of a feature normally generated by wear, such as a callus, or a pronounced muscle attachment, is strongly selected for. Individuals who develop it earlier due to genetic inclination to respond strongly to wear perform better than those who respond weakly and develop the feature slower, later in life (Waddington 1953). By this process, the response of an organism to its environment, be it paedomorphosis or paramorphosis, can be produced earlier and earlier in development. Newly born or juvenile animals already bearing features normally developed due to wear and tear have an edge over those who have to generate their response on the ancestral time scale (Waddington 1953). In some regards, the ability to quickly fix acquired characters into developmental pathways is as much an object of selection as any other trait. Selection on a developmental threshold is a permit for evolution, just like variability.

Likewise, the ability to pick between several different phenotypes during development is a trait selected on, but not one visible in an individual animal. In these taxa, environmental conditions during development and early life can trigger alternative developmental pathways which produce phenotypes better fitted to

particular environments. In an environment which oscillates between being resource rich and poor, this is a massive advantage. Many even toed ungulates exhibit this phenomenon. Deer fed a diet rich in fat and nutrients will produce a generation of large offspring, and stags in this generation will develop the best antlers and compete fiercely for the right to mate. Deer born to starving mothers, however, will be small, mean survivors that waste little energy on secondary sexual characteristics. Built to sustain, they keep the population alive when resources are scarce. These species' vastly different phenotypes, their dispersal and maintenance forms, are built into their genomes. Pathway changes are triggered by simple molecular switches such as the smell of smoke, for a forest fire means lush undergrowth the following spring (Geist 1989).

An enhanced ability to change phenotype through altering developmental timing, especially in response to environmental forces, is termed plasticity, and members of Canidae are known to have exceptionally plastic skulls. They possess several phenotypic modes, are also plastic, and critically, are able to pass on their responses through assimilation. One need only look at the range of skull shapes seen in domestic dogs to understand their capacity for variation (Schoenebeck and Ostrander 2013).

If wild canids possess even half the flexibility of domestic dogs, it is no surprise *V. vulpes* has done so well in so many places. If genetic assimilation is coming into play, or the retention of multiple pathways, then foxes, especially the

red fox, carry with them a powerful genetic toolbox. By virtue of their variability, they present plenty of options. By virtue of plasticity and genetic assimilation, they can cope with change. Should they draw on alternative phenotypic pathways, then they enter new situations equipped to capture the variations which best suit survival, or produce offspring already adapted to that environment. It is no wonder they excel at adapting to new locations. The adaptations they rely on to change shape are not fresh – they are thousands of years old, and have already passed the test.

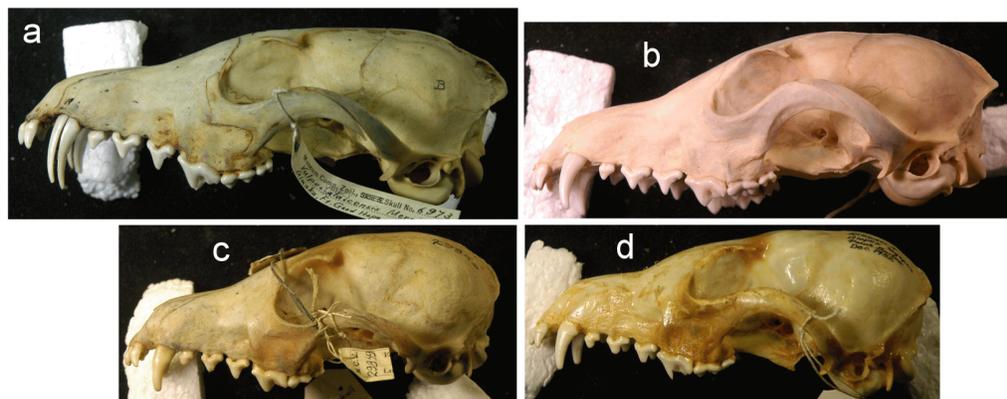


Figure 1. Comparison of *V. v. alascensis* (a), *V. v. fulva* (b), *V. l. groenlandicus* (c) and *V. l. lagopus* (d) skulls. Note the large sagittal crests present in *V. vulpes* and rounded skulls of *V. lagopus*. *V. v. alascensis* has a long muzzle and the others, including this particular *V. v. fulva*, have skulls with beaked profiles due to the angle at which their snout joins their forehead.

The Natural History of *Vulpes vulpes*, American Immigrant

The modern red fox boasts a cosmopolitan distribution and 45 subspecies, ranging from the plain-looking *V. v. anatolica*, which lives in Asia Minor, in the species' original range, to *V. v. arabica*, a racy, sleek, long-legged desert form, to

V. v. cascadenis, an American montane subspecies that is usually grey instead of red, to the quintessential red fox, *V. v. vulpes*, found in Russia and Central Europe, described by Linnaeus in 1750 (Larivière and Pasitschniak-Arts 1996).

How *V. vulpes* achieved its impressive range is due to an adaptability apparently not present in even its closest relatives. *V. vulpes* evolved where the first fox was found, in the arid lands of the Middle East, North Africa, and Asia Minor. The earliest known fox is *Vulpes riffautae*, from 7 Ma. The genus' earlier evolution may have occurred in Asia in the late Miocene, after small North American canids crossed onto the continent, but fossils corroborating this theory have not been found (Szuma 2008). Out of Africa and into Europe went *V. alopecoides*. 3.0-2.0 Ma, *V. alopecoides* roamed Villafranchian Eurasia. *V. alopecoides* may be the ancestor or sister taxon to all extant *Vulpes*. Though small, its teeth resembled modern *V. vulpes*'s. A related species, *V. chikushanensis* was found in China, but as DNA and morphological evidence points to the Middle East as the heart of *Vulpes* diversification, *V. alopecoides* is a better candidate (Kurtén 1968; Szuma 2008). The earliest red foxes appear in D-Holsteinian deposits in Asia Minor laid down 0.7 Ma (Kurtén 1968). Red foxes first appear in North America in the Sangamonian Stage, 132,000 years ago, before the last ice age (Kurtén and Anderson 1980). Molecular data implies *V. vulpes* arrived in North America earlier in the Pleistocene, through two immigration events, one following the Illinoian glaciation, which corresponds

with the oldest North American fossils, and again following the Wisconsin glaciation. The populations involved in these migrations were different, and diverged from one another 400,000 years ago while still living in Eurasia (Aubry et al. 2009). The red fox's closest relatives, on the other hand, remain in Africa (Lindblad-Toh et al. 2005).

The red foxes of northern climates tend to be large, well-furred, and sometimes, rather sexually size dimorphic, for a canid, while those from arid regions tend to be slight and smooth coated (Szuma 2008 and Lariviere and Pasitschniak-Arts 1996). *V. vulpes* is a species that follows Bergmann's rule almost to a T, forming North-South clines of descending size in both continents it naturally colonized (Szuma 2008). Their variability extends to their diet and habitat choice. The modern red fox dines not only on the expected fare of a wild canid – small mammalian prey – but also on birds and their eggs, insects, fruits and seeds, and human garbage, depending on what is most readily available. They prefer a mixed habitat with multiple sources to exploit as opposed to pure forest. This affection for patchy habitat and willingness to dine on scraps has allowed them to populate suburbia to an extent no other canid besides the domestic dog has managed (Lariviere and Pasitschniak-Arts 1996). Their plasticity is obvious in the range of places they inhabit, forms they take, and food they take, but is more evident still when the speed at which they colonize changing landscapes is examined in detail.

The North American red foxes, because of their dispersal history, form two large, genetically distinct clades, Holarctic and Nearctic. The Holarctic clade forms a cline roughly surrounding the pole with Palearctic European red foxes (Stratham et al. 2012). As originally described by Churcher in 1959, the cline included foxes in Western Europe and Eastern North America. However, the cline is better defined as containing the subspecies which cover the eastern portion of the Eurasian range and those found in Alaska and Western Canada. Western Europe's *V. vulpes* was not part of the eastern dispersal – obviously – and the foxes in Eastern North America are actually members of Nearctic clade, which diverged from the Holarctic clade 400,000 years ago, and entered North America before the Holarctic foxes, whose descendants form the subspecies which do fit the cline (Staham et al. 2012). Molecular data shows the Nearctic clade was the first to cross the Bering Strait, after the Illinoian glaciation. However, during the Wisconsin glaciation they were forced downwards and became isolated in Eastern Canada and montane regions in the West, which served as northern and southern refugia during that ice age. When the ice receded, a second wave of Eurasian foxes recolonized the Northwest (Aubry et al. 2009). The two major clades became three: the Holarctic, the Eastern, and the Mountain, which are reflected in molecular markers found in the mitochondrial DNA of modern North American red foxes. They developed in isolation from one another until European colonization of the Atlantic coast. European settlers greatly changed the

landscape, converting tract after tract of forest into farmland. The new habitats created suited the red fox, and they poured out of Canada. From the east coast, they spread pace for pace with settlers to reach the west. In less than 500 years, the Widespread clade developed from the Eastern (Staham et al. 2012). Mitochondrial DNA shows the three Nearctic clades rarely mingle with one another, even where the range of Eastern subspecies overlaps the range of montane subspecies derived from the especially isolated Mountain clade. The montane subspecies are threatened by habitat loss, but fortunately, not by interbreeding with other *V. vulpes* (Perrine et al. 2007) However, it is unclear whether or not Holarctic-derived subspecies cross with Eastern and Widespread Nearctic-derived subspecies in Canada (Aubry et al. 2009).

Because of the complex way in which red foxes colonized North America, their taxonomy has understandably been debated. Originally, due to differences in phenotype, such as the predominance of black and grey in some populations, and larger size, the North America red fox was declared a separate species, *V. fulva*, by Desmarest (1820). However, the validity of his specimens was questionable – it was attested the skull he based his work on was from a grey fox (*Urocyon*), for example, not a red fox (Churcher 1960). The validity of *V. fulva* thus remained contest until Churcher published the discovery of the cline in 1959. Then, the name was retired and all red foxes were reunited under *Vulpes vulpes*, despite the fact that those populations later found to descend from the Nearctic clade did not

fit the cline well. Also, the sudden appearance of red foxes in the eastern United States was initially attributed to the spread of European foxes intentionally introduced by settlers for sport hunting in the 1700s, as is the case in Australia (Kamler and Ballard 2002). Up until the publication of a 2009 mitochondrial DNA study found absolutely no Eurasian haplotypes among any North American fox and exposed the phylogeny of the clades, it was believed most foxes in the United States were non-native (Aubry et al.). Follow up studies have confirmed their results (Stratham et al. 2014). No introduced red foxes found a foothold on the continent, and thus, the North American populations are discontinuous with the Eurasian populations. Given this, and how little interbreeding there is between the North American clades themselves, it may be worth resurrecting *V. fulva* for descendants of the Eastern clade and perhaps designating the Mountain foxes a species of their own, as the Eastern and Mountain clades remain reproductively isolated by altitude even where their ranges overlap (Perrine et al. 2007).

Currently, the epithet *fulva* belongs to a subspecies of Eastern red fox, the very one which was originally believed to be of European origin. *V. v. fulva* is notably polymorphic, even for a red fox, and unsurprisingly, is able to utilize a wide variety of habitats present in its range as a result. While all red foxes can be said to specialize as generalists, *V. v. fulva* excels in this regard (Ables 1975).

While *V. v. fulva* epitomizes the term plastic, its somewhat distant relative, *V. v. alascensis*, does not. Native to Alaska and parts of Canada, this subspecies of

red fox is uniformly large and sexually dimorphic, all the way down to the level of its dentition. In the North American Holarctic population, an East-West gradient exists in addition to the North-South size gradient. *V. v. alascensis* is thus among the largest of the red foxes. Perhaps due to their size alone, their teeth, too are fixed to be larger than they are in other populations where tooth size is less conserved, as is size (Szuma 2008). *V. v. alascensis* also has the distinction of being the subspecies from which most captive raised foxes derive from, as their large size and richly colored, plush fur appealed to fur farmers across the globe. The silver (black or grizzled, with a white-tipped tail) variation is most popular in the fur trade (Bailey 1993).

The Natural History of *Vulpes lagopus*, Arctic Icon

Unlike *V. vulpes*, *V. lagopus*' distribution is restricted to the Arctic Circle. However, its population is only periodically discontinuous. The Arctic fox is small, to lower its caloric requirements, and built to reduce surface area, an adaptation which prevents heat loss. Its extremities, including its ears, legs, and snout, are short and round compared to most red foxes. They are noted to have weaker skulls than other foxes, but are sexually size dimorphic (Audet et al. 2002). Their skulls are noted to have shorter and slightly broader snouts than red foxes, and their mandibles are more compact (Figure 1) (Fraçkowiak et al. 2013). They boast extreme cold tolerance. Arctic foxes survive winter in the farthest northern reaches of their range thanks to a critical temperature of -40 °C, a thick,

insulating undercoat, subcutaneous fat deposits, and peripheral vasoconstriction. Warming retes keep their paw pads from freezing. Metabolic depression enables them to prevent energy wastage during periods of extreme weather when hunting is impossible. Their pelt is white or blue in winter, and grey or brown in summer, so that the animal is always camouflaged (Audet et al. 2002). Depending on where they live relative to the ocean, their diet and behavior varies. Foxes dwelling close to coastlines feed on seabirds, their eggs, and carcasses washed up on the shore. Inland foxes, like many arctic carnivores, largely depend on the lemming for sustenance. As lemming populations can vary dramatically from year to year, inland Arctic foxes are known to migrate periodically to seek areas in which the lemming population has not yet been depleted (Dalén et al. 2005). The same metabolic depression they employ during winter can activate during periods of food shortage in summer should nothing be found (Audet et al. 2002). Populations which adjust to human presence take readily to scavenging garbage, and the leavings of hunters and fishermen, like red foxes do (Kapel 1999). But, their dentition is adapted for hypercarnivory, as prior to human settlement, the Arctic offered little year-round nutrition besides meat. Their canine teeth are large, their molars simple, and their jaws deep, compared to other foxes (Wang et al. 2014; Valkenburgh et al. 2002). The Arctic fox's adaptations enable it to survive in one of the harshest environments on Earth. It stands as an example of evolutionary triumph, if specialization to a unique, harsh niche is the metric by

which triumph is measured.

Due to the degree to which it has specialized, the Arctic fox was once the sole member of its own genus, *Alopex* (Audet et al. 2002). However, based on morphology, later authors argued it belonged in *Vulpes*, much as the social, maned, solid tawny (and thus highly divergent) lion belongs in the genus *Panthera* with the other big cats, who are solitary, unadorned, and cryptically marked (Wei et al. 2011). In both cases, the divergent member is similar to the rest of the genus once the skin is stripped away. However, it was not until molecular based phylogenies of Canidae were produced that the placement of the Arctic fox within *Vulpes* was proven. It resides closest to the kit (*Vulpes macrotis*) and swift foxes (*Vulpes velox*), and especially close to the Tibetan sand fox (*Vulpes ferrilata*) on a separate branch from *V. vulpes* (Lindblad-Toh et al. 2005; Wang et al. 2014). Despite this, the name *Alopex lagopus* remains in common use.

Like *V. vulpes*, *V. lagopus* probably descended from *V. alopecoides* (Kurtén 1968). Its most recently known fossil ancestor, *V. qiuzhudgingi*, was found in Pleistocene-era Tibet. The high plateaus of Tibet were the incubation sites of many lineages now found in the Arctic. When glaciation events caused cold climates to spread south to meet these high altitude mountain ranges, fauna preadapted to dwelling in year-round cold were able to disperse. *V. qiuzhudgingi*, though larger than the modern arctic fox, already showed strong signs of hypercarnivory (Wang et al. 2014). Where the glaciers spread, so did *V. lagopus*,

and when they receded to the pole, there they stayed (Kurtén 1968). The modern population's movements are still bound by glaciation. While red fox populations are divided by ice ages and able to spread during interglacial episodes, pack ice thick enough to re-form Beringia is required by *V. lagopus* for populations to mix. While *V. lagopus* is broken into subspecies by phenotype, molecular data shows recent mixing between all but the Icelandic population, which likely occurred during the last ice age. However, as the world is undergoing accelerated warming, New and Old World populations are currently divided and may become more fragmented even on the continents, perhaps permanently (Dalén et al. 2005). It is generally held that they lack the variation and adaptable nature of red foxes, and due to the extreme specializations they evolved to stay and succeed in their niche, southern expansion is thus impossible for them (Szuma 2008). As they have historically between glaciations, they will follow their shrinking habitat north until it is gone. The red fox may someday replace them (Szuma 2008).

Currently, eight subspecies are recognized, including *V. l. groenlandicus*, from Greenland, a population with the small, round phenotype typical to Arctic foxes, and *V. l. lagopus*, which ranges across Alaska and Canada (Audet et al. 2002). In both populations, coastal and inland ecotypes exist (Dalén et al. 2005). Like *V. v. alascensis*, *V. l. lagopus* is the source of most farmed members of its species, due to the blue winter coats found in some coastal and island populations, which were once quite fashionable (Bailey 1993).

When Red and White Unite

Where *V. l. lagopus* and *V. v. alascensis* overlap in Alaska, *V. v. alascensis* ousts the arctic fox. As the two have the same dietary resources, they clash over territory. Red foxes are observed to be the aggressors. Their readiness to skirmish may be due to their greater need for resources, as their larger size and lack of metabolic adaptations to cold and periods of semi-starvation means they require 90% larger home ranges than Arctic foxes to survive in the north, especially in areas where human waste is not readily available. As Alaskan red foxes are substantially larger than Arctic foxes, Arctic foxes avoid confrontation with them and typically run when chased from dens or food by their congeners. However, several kills of arctic foxes by red foxes have been reported (Hersteinsson and MacDonald 1992). In one recorded kill, the Arctic fox was eaten by the red (Pamperin et al. 2006).

The conservation of sexually dimorphic larger teeth in *V. v. alascensis* noted by Szuma may be related to competition between the species. Red foxes typically form mated pairs in resource poor areas, and the male, as in many species, is primarily responsible for defense of the territory. The larger and more impressively equipped the male, the more successful his efforts will be, as fox threat displays are designed to show off body size and the teeth (Szuma 2008). However, given the energetic needs of Alaskan red foxes, this is an evolutionary catch-22: to secure enough resources, *V. v. alascensis* must be large enough to

scare away competitors of its own species as well as Arctic foxes, but to be larger, they must eat more, and that will require more territory. The larger the territory, the more difficult it is to defend. There exists some ceiling at which territory size becomes indefensible, and metabolic demands requiring more land than this cannot be met. This is an unsustainable evolutionary trend and some authors predict the red fox will never be able to breed throughout the arctic fox's range because it is simply too big to be sustained there. However, they appear capable of pushing the Arctic fox out of areas where warming temperatures and increasing amounts of urbanization boost both food resources and suitable habitat (Hersteinsson and MacDonald 1992). Calorie-dense human food allows for smaller ranges and increased population size and density in both foxes, but red foxes are more willing to use roads and buildings for travel and denning (Harris and Rayner 1986, Rudzinski et al. 1982). So in warming, urbanizing areas, their large size remains an advantage, and they are already prevailing in regions meeting those conditions (Hersteinsson and MacDonald 1992).

The antagonistic behavior of red foxes towards arctic foxes extends to captivity, even when the red fox subspecies is not one naturally sympatric with *V. lagopus*, which is interesting as red foxes usually give way to other canids such as the grey fox, which like the Arctic fox, is smaller than it is (Rudzinski et al. 1982). However, artificially inseminated hybrids between *V. v. alascensis* and *V. l. lagopus* are produced in the fur trade, primarily in Eastern Europe, for their pelts.

The hybrids, though sterile, are large and fast developing, with features intermediate between their parents. Their fur is plush, like an Arctic's, but due to the influence of the red fox, they are bigger (Mälkinen and Gustavsson 1982). Molecular studies report that while the parent species have different numbers of chromosomes ($2n = 34-42$ in *V. vulpes* and $2n = 48-50$ in *V. lagopus*), the chromosome counts are different mainly due to the evolution of two-armed chromosomes going differently in each species, as well as translocations and inversions found in some, but not all individuals. The contents of each genome are more or less the same, however, so the hybrids have no problems besides the sterility associated with the meiotic failure common in hybrids whose chromosomes are not evenly paired (Mälkinen and Gustavsson 1982). The hardiness of the red fox to polymorphic chromosomes is an example of not only its variability, but its tolerance thereof, something the Arctic fox apparently does not have on a chromosomal level. About 20% of gene products differ between reds and Arctics; the blood cells of hybrid females contain Glucose-6-phosphate dehydrogenases that function better at different pHs depending on which X chromosome was active in the hemopoietic tissue that produced the cell. Despite this, they lead healthy lives, indicating along with the low percentage of protein differences that although the red fox and Arctic fox diverged from one another long ago, they are not so different that they cannot be accepted as members of the same genus (Serov and Zakijan 1977; Serov et al. 1977).

The Alaskan Question

If *V. v. alascensis* is likely to force *V. l. lagopus* into a restricted, fragmented range, its natural plasticity has likely permitted its success thus far. However, their overall morphology and dentition suggest a loss of variability is taking place as the population adapts to the harsh requirements for success that northern climates place on predators. The Arctic fox bears signs of the same transformation from generalist to specialist, though its adaptations were acquired before it reached the Arctic Circle. *V. v. alascensis*, however, is adopting a different strategy than the Arctic Fox did. Rather than shrink to conserve energy, the Alaskan red fox has grown larger. Were it not for global warming and urbanization, this path would have proven unfruitful for them, and depending on how much more the climate changes, their size may keep them from surviving in the highest, coldest altitudes and latitudes in which the Arctic fox is found. Where their ranges currently overlap, males red foxes use their large size and the threat of their large teeth to boost the effectiveness of threat displays and sometimes, to kill competing Arctic foxes outright.

As teeth develop in the skull and jaw, part of their morphology is dictated by the bones around them. Thus, if *V. v. alascensis* is truly moving towards a more conserved form, their skull and jaw shape should be less variable than *V. v. fulva*'s, and if behavioral studies are correct, should also correlate to size and sex. However, there is more to surviving Alaska than the protection of territory. Two

of the Arctic fox's skeletal traits are a short muzzle and a deep jaw. Their shorter muzzles and more paedomorphic skulls lose heat more slowly than typical or paramorphic skulls, as they present a smaller surface area to volume ratio. Their deep jaws make up for the smaller muscular attachment sites caused by paedomorphosis and increase their bite force to make their almost exclusively carnivorous diet easier.

While comparisons of dimensions have been made between red and Arctic foxes, morphometric analysis independent from scale has not been previously performed. As these populations are rapidly changing, a look into adaptive shape of the skull itself may provide insight into the current success of *V. v. alascensis* beyond offensive and defensive capabilities and determine whether the Alaskan red fox is truly replacing the Arctic fox within its niche as a small, cold hardy carnivore, or if its success in Alaska is strictly due to its broader diet and offensive capabilities.

MATERIALS AND METHODS

A total of 49 skulls were used in this study, and a combination of physical and digital methods were used to gather data from them. Intact skulls with subspecies, location, and sex data were used when available. Nineteen were *V. lagopus*: ten were wild *V. l. lagopus*, two were captive bred *V. l. lagopus*, six were wild *V. l. groenlandicus*, and one was a *V. lagopus* of unknown subspecies and locality. Twenty-eight were *V. vulpes*: 12 were wild *V. v. alascensis*, 14 were wild *V. v. fulva*, and two were *V. vulpes* of unknown location and subspecies. Two were captive bred *V. vulpes x lagopus*. Eighteen were female, 21 were male, and ten were of unknown sex (Table 1). All were adults based on fusion of the skull but exact age data were not available (Churcher 1960). All wild *V. l. lagopus* and *V. v. alascensis* were treated as sympatric as *V. v. alascensis*' range completely overlaps the locations where *V. l. lagopus* were collected (Lariviere and Pasitschniak-Arts 1996). All but one wild *V. l. lagopus* were from Alaska. *V. v. fulva* was chosen as an outgroup, as its range does not overlap with an arctic foxes and it is noted to be a very variable subspecies of red fox, in contrast to *V. v. alascensis* (Ables 1975). *V. l. groenlandicus* was also selected as an outgroup as it is not sympatric with any red foxes (Audet et al. 2002).

Photographs of each specimen's cranium were taken from dorsal, ventral, and right and left lateral views. When available, photographs of the right and left

Specimen Data				
<i>Specimen ID</i>	<i>Species</i>	<i>Location</i>	<i>Sex</i>	<i>CBL</i>
MCZ29849	<i>V. l. groenlandicus</i>	Ymer Island, Greenland	Female	108.9
MCZ29850	<i>V. l. groenlandicus</i>	Ymer Island, Greenland	Male	113.2
MCZ29851	<i>V. l. groenlandicus</i>	Kejser Franz Joseph Fjord, Greenland	Male	116.1
MCZ29852	<i>V. l. groenlandicus</i>	Ymer Island, Greenland	Male	118
MCZ29853	<i>V. l. groenlandicus</i>	Ymer Island, Greenland	Male	113
MCZ58133	<i>V. l. groenlandicus</i>	Cape Stosch, Greenland	Unknown	NA
MCZ21808	<i>V. l. lagopus</i>	Baffin Island, Nuvanut, Canada	Female	120.4
MCZ46599	<i>V. l. lagopus</i>	Saint Lawrence Island, Alaska	Female	108.9
MCZ46600	<i>V. l. lagopus</i>	Saint Lawrence Island, Alaska	Female	116.7
MCZ46601	<i>V. l. lagopus</i>	Point Barrow, Alaska	Male	199.3
MCZ46602	<i>V. l. lagopus</i>	Point Barrow, Alaska	Female	116.7
MCZ52835	<i>V. l. lagopus</i>	Barrow, Alaska	Male	121.8
MCZ52836	<i>V. l. lagopus</i>	Barrow, Alaska	Male	114.9
MCZ52837	<i>V. l. lagopus</i>	Barrow, Alaska	Male	126.1
MCZ52838	<i>V. l. lagopus</i>	Saint Lawrence Island, Alaska	Female	118.5
MCZ52839	<i>V. l. lagopus</i>	Saint Lawrence Island, Alaska	Male	121.2
MHCVv003	<i>V. l. lagopus</i>	Captive	Unknown	136.3
MHCVv1002	<i>V. l. lagopus</i>	Captive	Unknown	140.1
MHCV1001	<i>V. l. unknown</i>	Unknown	Unknown	115.3
MCZ21836	<i>V. v. alascensis</i>	Unimak Island, Alaska	Female	138.3
MCZ45253	<i>V. v. alascensis</i>	Seward Peninsula, Alaska	Unknown	136.4
MCZ46574	<i>V. v. alascensis</i>	Chandler Lake, Alaska	Male	140.2
MCZ46575	<i>V. v. alascensis</i>	Chandler Lake, Alaska	Female	129.9
MCZ46576	<i>V. v. alascensis</i>	Anactuvuk Pass, Alaska	Female	141.4
MCZ46577	<i>V. v. alascensis</i>	Noatak River, Alaska	Male	136.9
MCZ46578	<i>V. v. alascensis</i>	Arctic Village, Alaska	Male	138.7
MCZ46579	<i>V. v. alascensis</i>	Arctic Village, Alaska	Female	138.5
MCZ46580	<i>V. v. alascensis</i>	Glenn Highway, Mile 170, Alaska	Male	139.1
MCZ46581	<i>V. v. alascensis</i>	Tyrone Lake, Alaska	Female	128
MCZ6972	<i>V. v. alascensis</i>	Yukon River, Alaska	Female	132.8
MCZ6973	<i>V. v. alascensis</i>	Fort Good Hope, Alaska	Male	134
MCZ52822	<i>V. v. fulva</i>	Dutchess County, New York	Female	135.1
MCZ52823	<i>V. v. fulva</i>	Dutchess County, New York	Male	133.7
MCZ55574	<i>V. v. fulva</i>	Brunswick, Maine	Female	130.3
MCZ55575	<i>V. v. fulva</i>	Manchester, Maine	Female	120

MCZ58772	<i>V. v. fulva</i>	Ferrisburg, Vermont	Male	115.7
MCZ58773	<i>V. v. fulva</i>	Mendon, Vermont	Male	133.3
MCZ61731	<i>V. v. fulva</i>	Andover, Massachusetts	Female	124.5
MCZ64670	<i>V. v. fulva</i>	Narragansett, Rhode Island	Male	126
UM1268	<i>V. v. fulva</i>	Campbell, New York	Male	124.4
UM1269	<i>V. v. fulva</i>	New York	Female	121.8
UM1270	<i>V. v. fulva</i>	Tyrone, New York	Male	135.4
UM2181	<i>V. v. fulva</i>	Westfield, Massachusetts	Unknown	129.7
UM4033	<i>V. v. fulva</i>	Gosnold, Massachusetts	Unknown	NA
UM4253	<i>V. v. fulva</i>	Hadley, Massachusetts	Male	NA
MHCv001	<i>V. v. unknown</i>	Unknown	Unknown	127.9
MHCv002	<i>V. v. unknown</i>	Unknown	Unknown	127.7
MCZ51421	<i>V. vulpes x lagopus</i>	Captive	Female	141.1
MHCv001	<i>V. vulpes x lagopus</i>	Captive	Unknown	134.7

Table 1. Data for each specimen. Specimen identification names (IDs) contain the prefix of the institution each specimen is property of. MCZ prefixed specimens belong to the Museum of Comparative Zoology at Harvard University, UM prefixed specimens belong to the Natural History Collection at University of Massachusetts Amherst and MHC prefixed specimens belong to Mount Holyoke College. IDs are those given by respective institutions except for those from Mount Holyoke College, which do not have IDs. IDs were created for these specimens for the purposes of this study. Subspecies, location of collection, and sex are as given by data provided with each specimen. Condylbasal length (CBL) is given in millimeters (mm).

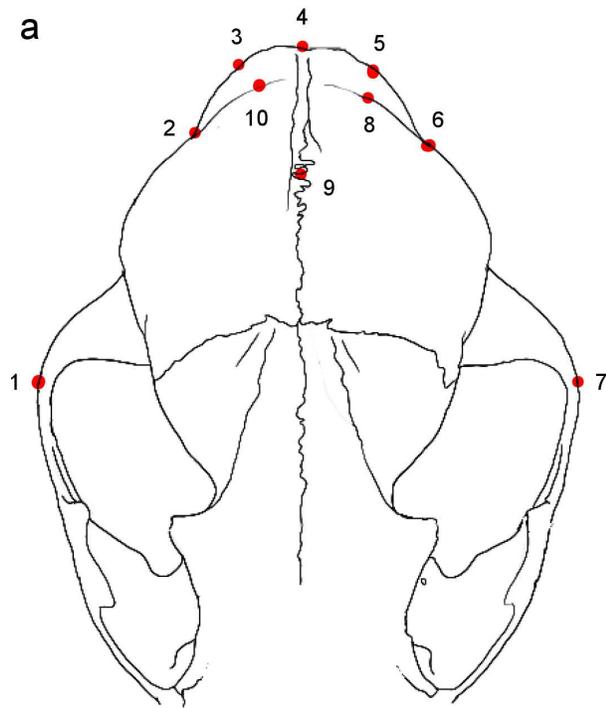
labial sides of the jaw were taken as well.

The width of the palate at its maximum breadth was obtained using digital calipers. This measurement was used to scale images in ImageJ (Version 1.49v; Schneider and Rasband, 2012). From the scaled ventral view of each specimen, the condylbasal length (CBL) was determined. CBL is an accurate reference to body mass, and thus, size, but the maximum breadth of the palate was more reliably repeatable in the lab, so this was taken manually instead of the CBL.

Landmarks and semi-landmarks were chosen which would result in wire

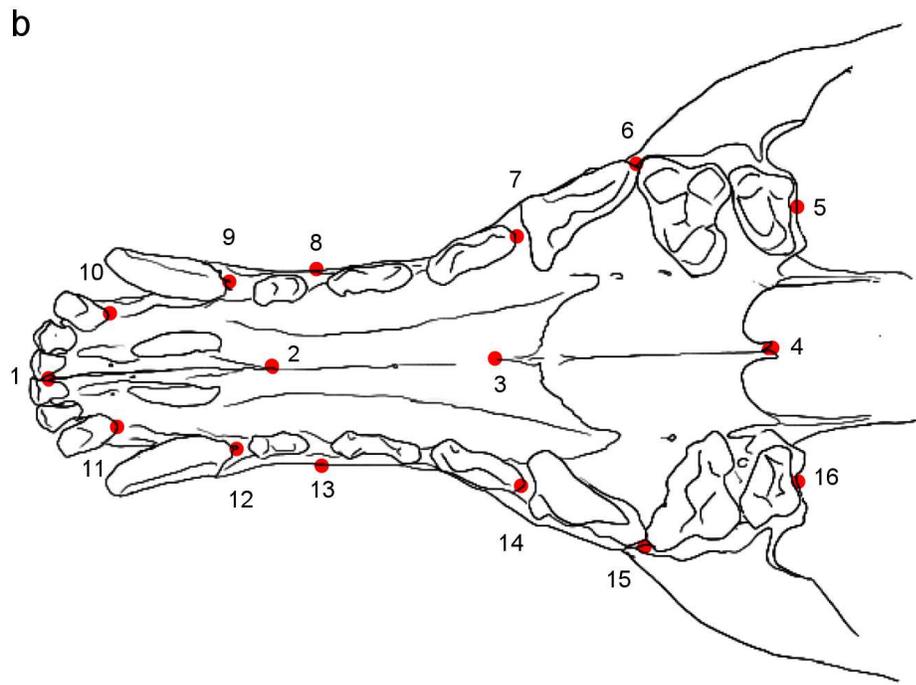
frames which simplified but readily displayed differences between specimens. Landmarks are homologous structures found in all compared groups; semi-landmarks are points which aid in describing a shape but may not be homologous between individuals, such as the narrowest part of a structure, or the point between two true landmarks. Eight landmarks and two semi-landmarks were chosen that described the sagittal crest and width of the skull in its dorsal aspect; 11 landmarks and three semi-landmarks defined the labial aspect of the jaw; 13 landmarks and six semi-landmarks described the snout portion of the lateral aspect of the cranium; 12 landmarks and 4 semi-landmarks illustrated the palate (figure). Using software tpsUtil (Tps Utility Program, version 1.68; Rohlf, 2016), .tps files for each set of landmarks were built. Specimens were omitted from certain sets if they lacked critical landmarks due to severe damage, or if the images were unusable. Only the left sides were used to create sets for the lateral snout and labial jaw as a greater number were intact. Foxes, like most animals, display some asymmetric growth in their skulls, which can be indicative of genetic fitness. However, because that was not the focus of this study, this source of variation was omitted. 47 specimens were included in the dorsal set, 41 in the jaw set, 45 in the lateral set, and 47 in the ventral set.

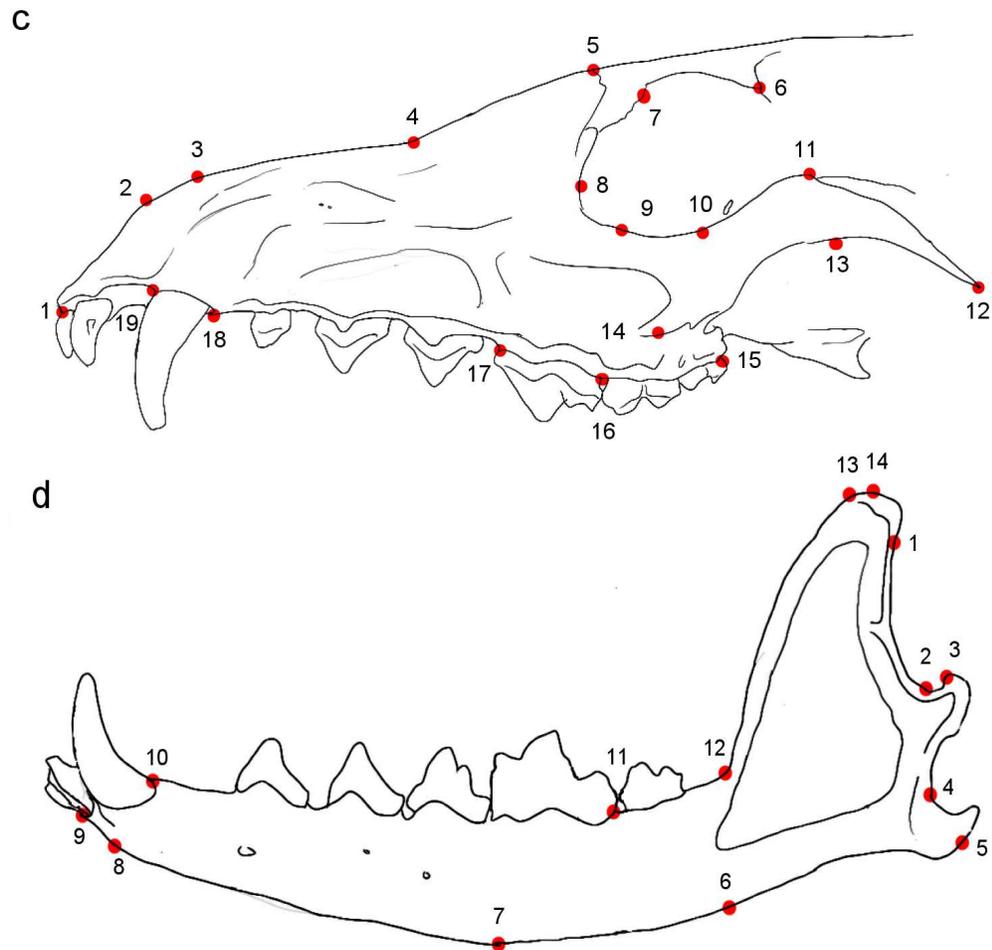
Landmarks were digitized using tpsDig (tps Dig2, version 2.22; Rohlf, 2015). Where landmarks were obscured due to curatorial procedures, such as glossy varnish, residual tissue, or twine holding jaws together, or when they were



missing due to damage, they were marked missing.

The resulting .tps files were imported to MorphoJ (Version 1.60d; Klingenberg, 2011) along with data for subspecies, location, sex, and CBL. From these files, covariance matrices were created. These matrices





were used to compute principal

Figure 2. Landmarks and semi-landmarks. In (a), the sagittal crest is depicted with 1), the right widest point on the zygomatic arch, 2), the lateral-most point on the righthand side of the sagittal crest, 3), the midpoint between points 2 and 4, 4), the posterior-most point of the sagittal crest, 5), the midpoint between points 4 and 6, 6), the lateral-most point on the lefthand side of the sagittal crest, 7), the widest point of the zygomatic arch on the left side, 8), the midpoint of the anterior lefthand border of the sagittal crest, 9), the most anterior point of the sagittal crest, and 10), the midpoint of the anterior righthand border of the sagittal crest. 1, 3, 5, 7, 8, and 10 are semi-landmarks. In (b), the palate is illustrated by 1) the anterior-most point of the incisive bone, 2) the postior-most point of the suture between the incisive bone and the palatine bone, 3) the anterior-most point of the suture between the palatine bone and the vomers, and 4) the most posterior point of the vomers. 5) is the most posterior edge of the last molar on the lefthand side, 6) the widest point of the palate, 7) the posterior edge of the 3rd premolar, 8) the narrowest point of the palate, 9) the posterior edge of the left canine's socket, and 10) the posterior edge of the 3rd left incisor's

socket. 11-16 mirror 5-10. In (c), the lateral aspect of the snout is described by 1) the anterior-most point of the incisive bone, 2) and 3), the upper and lower boundaries of the nasals, 4), the posterior-most point of the nasals, 5) the uppermost point of the maxillary-frontal bone suture, and 6), the posterior-most point of the postorbital bone. 7-10 are semi-landmarks describing the orbit. 11) is the uppermost point on the zygomatic-squamosal border, 12) the lowest, 13) the midpoint of the underside of the zygomatic arch, 14) the lowest point of the zygomatic arch, 15) the posterior most edge of the tooth row, 16) the posterior edge of the upper carnassial, 17) its anterior edge, and 18) and 19) the posterior and anterior edges of the canine tooth's socket. In (d), the labial aspect of the jaw is described by 1) the posterior end of the coronoid crest, 2) the mandibular notch, 3) the condyloid process, 4) the condyloid notch, 5) the angular process, 6) the anterior end of the masseteric line, 7) is a semi-landmark marking the deepest point on the body of the jaw, 8) is the base of the incisive roots, 9) the anterior most point on the dentary, 10) the posterior edge of the canine tooth's socket, 11) the posterior edge of the lower carnassial, 12) the point where the tooth row angles up into the coronoid process, 13) marks the anterior-most point of the coronoid crest, and 14) marks the highest point on the coronoid crest.

component analyses for each set. Slider and link files for each .tps file were created in tpsUtil. These were used along with the original .tps files to build relative warps in tpsrelw (Relative warps, version 1.62; Rohlf, 2016). These were examined in tpsRegr (tpsRegr, version 1.43; Rohlf, 2016) and compared to comparative wireframe graphs output by MorphoJ to connect the three most significant principal components (PCs) in each set to the features whose variation they account for. For each PC, correspondence of PC values to subspecies were examined graphically.

In R (Version 3.2.4 Revised; R Core Team, 2013), multivariate analysis of variance (MANOVA) tests were run for subspecies, sex, and CBL against PC1, PC2, and PC3 for each set of landmarks. The correlation or lack of correlation for each independent variable was checked against variability as a whole and for each specific PC.

RESULTS

Principal Components

<i>Percentage of Variance Accounted for by Different PCs</i>				
	<i>Principal Component</i>			
Region	PC1	PC2	PC3	Total
Sagittal Crest	52.867	30.971	5.901	89.739
Palate	57.733	29.955	8.486	96.174
Snout	46.711	12.88	11.644	71.235
Jaw	39.777	32.901	19.095	91.773

Table 2. Percentage of variation accounted for by different principal components.

The three principal components accounting for the most variation in the sagittal crest and zygomatic arch width accounted for 52.867%, 30.971%, and 5.901% respectively, for a total of 89.739% of the total variation in those structures (Table 2). PC1 described the length of the portion of sagittal crest that runs down the midline of the dorsal surface. PC2 mainly related to how far the distal ends of the lateral components of the crest fell from the midline. The posterior skulls of specimens with high values for both PC1 and PC2 appear almost boxy, due the projection of the sagittal crest behind the cranium. The value of PC3 relates to the overall width of the zygomatic arch. At high values, the zygomatic arch widens at the expense of the width of the crest and the depth of its lateral elements (Figure 3).

The principal components with the most shape variation in the palate accounted for 57.733%, 29.955%, and 8.486% of variation in that element, for a

total of 96.174% of palate variation (Table 2). PC1 and PC2 illustrate synergistic shape changes that compact the muzzle at higher values by elongating the incisive bone and consequentially shortening the vomers, as is the case with PC1, or elongating the incisive bone towards the posterior while extending the anterior border of the vomers rostrally to compensate, as PC2 does. PC3 is concerned with the overall width of the muzzle and the shape of the vomer's labial border. At

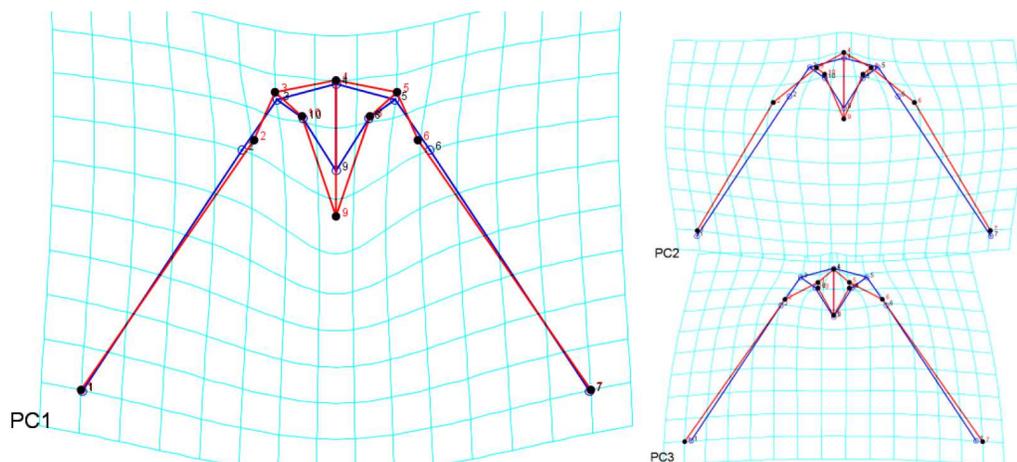


Figure 3. Principal components of variation in the sagittal crest 1-3. In all PC wireframe graphs, blue wireframes represent the starting shape, with the lowest values for the given PC; red lines

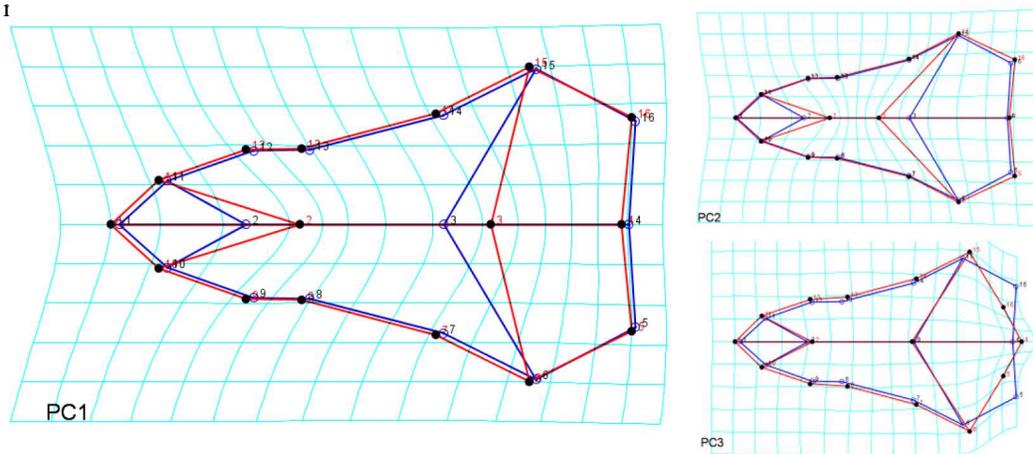


Figure 4. Principal components of variation in the palate 1-3.

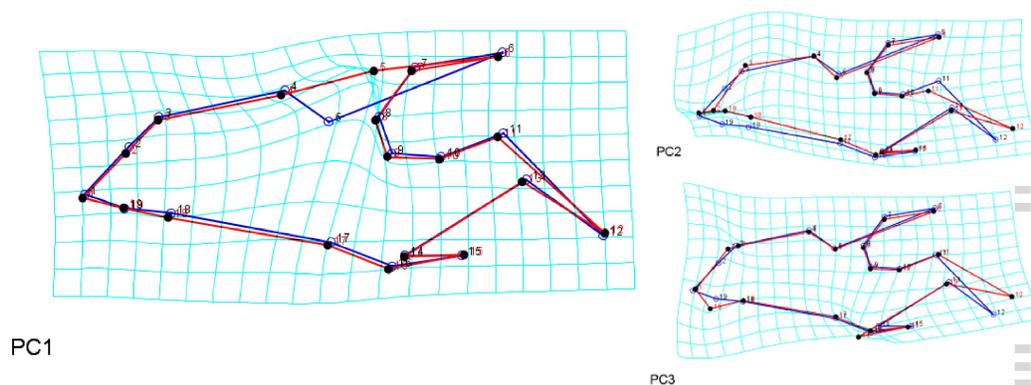


Figure 5. Principal components of variation in the snout 1-3.

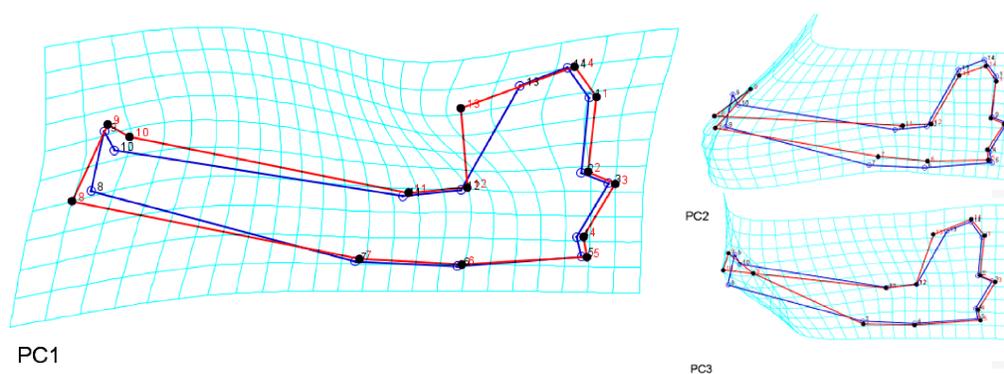


Figure 6. Principal components of variation in the jaw 1-3.

higher values, the muzzle is broader and the vomer bends at the carnassial tooth, resulting in the molar rows angling inwards instead of parallel to the midline (Figure 4).

Variation in the lateral aspect of the snout divides between PC1 (46.711%), PC2 (12.880%), and PC3 (11.644%), which together account for 71.235% of snout variation (Table 2). PC1 expresses how beaked and puppy-like the skull is. The higher PC1 is, the more smoothly sloping the transition from muzzle to forehead is. PC2 and PC3's values both relate to how bent the incisive, maxilla,

and zygomatic arch are in profile. Higher values of both components result in a more shallow curve in the arch. High values of PC1 decrease crimping of the muzzle, and high values of PC2 accompany the shallow zygomatic arch with a downwards twist to the rostral-most end of the muzzle (Figure 5).

In the jaw, PC1 accounts for 39.777% of variation, PC2 for 32.901%, and PC3 for 19.095% of variation, for a total of 91.773% of variation visible in the jaw viewed labially (Table 2). High values of PC1 are associated with a deeper, more robust jaw that does not taper, and a wide coronoid process that extends more anteriorly than one in a specimen with a low value for PC1. Jaws with high values for PC2 are straighter and narrower than those with low values. When PC3 is high, the rostral end of the dentary is narrow and the coronoid process inclines backwards somewhat more (Figure 6).

Trends by Subspecies

The value of dorsal PC1 tends to be low in the majority of foxes, though it can be much higher in some members of both Alaskan populations, *V. l. groenlandicus*, and hybrid foxes (Figure 7). Dorsal PC2 values skew somewhat higher for *V. vulpes* than for *V. lagopus* (Figure 8). Dorsal PC3 is highest in *V. l. lagopus* and its hybrid with *V. v. alascensis*, then in *V. l. groenlandicus* and *V. v. alascensis*, and lowest in *V. v. fulva*. However, the PC3 values for *V. l. lagopus* are spread over a wider range than in the other subspecies are (Figure 8). To summarize, long sagittal crests appear in both Alaskan subspecies and some *V. l.*

groenlandicus, but wider sagittal crests are more prominent in Alaskan red fox populations than in any arctic fox population, and wider zygomatic arches are found in arctic foxes, with the widest arches in the Alaskan population.

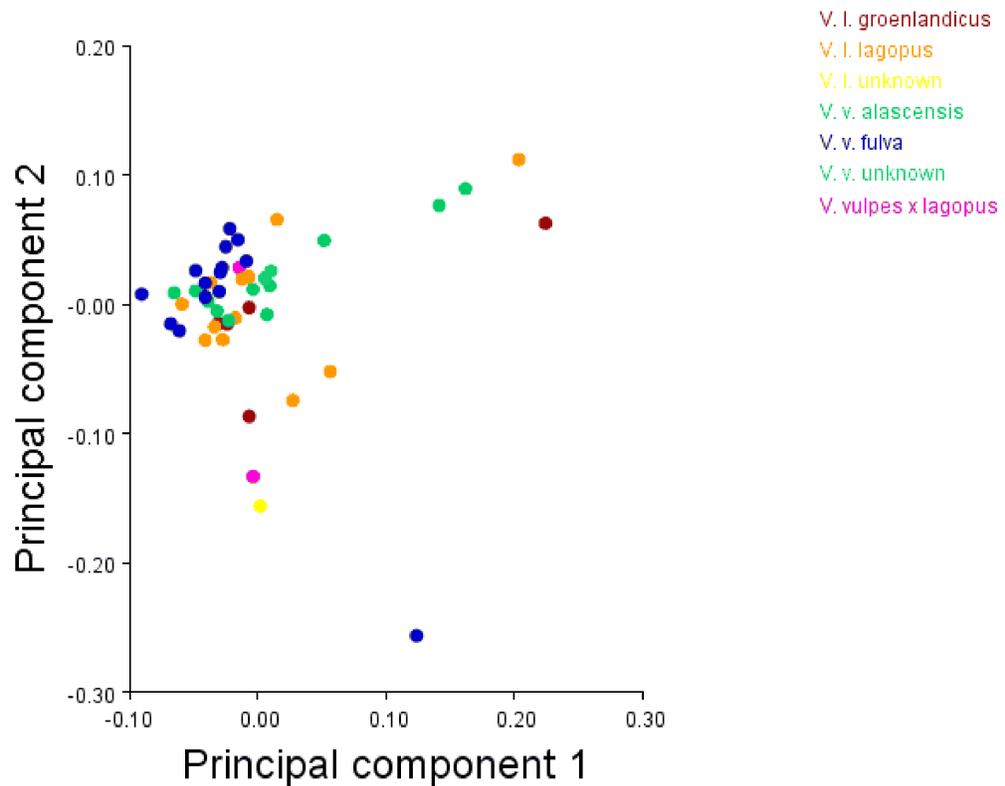


Figure 7. Comparison of dorsal PC1 and 2. Most foxes fall close to the mean.

The patterns of variation for ventral PC1 and PC2 are the same. Most foxes have average to slightly compact muzzles, a few *V. v. fulva* exhibit slightly to very elongate snouts, and although most *V. v. alascensis* and *V. l. lagopus* have average

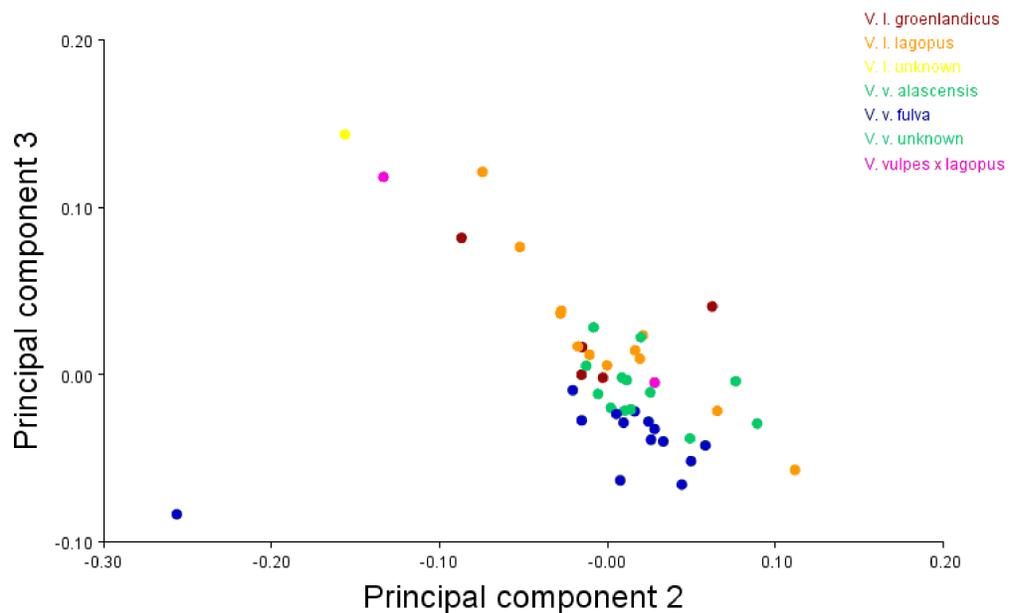


Figure 8. Dorsal PC2 values compared to dorsal PC3 values. PC3 value was correlated to subspecies ($p = 0.000002264$).

values for PC1 and PC2, two clusters with elongate muzzles group out from both subspecies. Both groups have low values for PC1. One group has low values for both PCs; the other group is more compact due to a higher value for PC2 (Figure 9). PC3 tends to be average, though slightly elevated values can be seen in both Alaskan subspecies and *V. v. fulva* (Figure 10).

The distribution of values for lateral PC1 is roughly bimodal. Some *V. v. fulva*, the hybrids, and most *V. l. groenlandicus* have low values, indicating their skulls are very beaked, while members of both Alaskan subspecies may be moderately beaked. Some *V. v. fulva*, the hybrids, and most *V. l. groenlandicus* have low values, indicating their skulls are very beaked, while members of both Alaskan subspecies may be moderately beaked. Most other *V. v. fulva* and Alaskan subspecies have more sloping skulls (Figure 11).

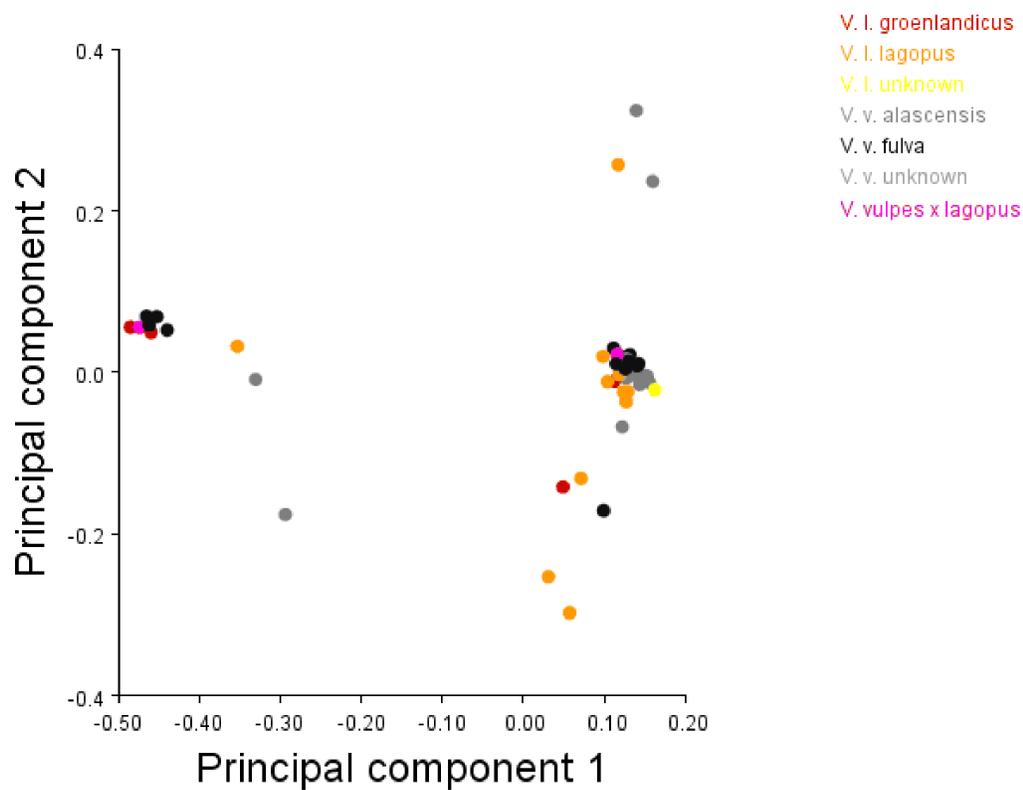


Figure 11. Principal components 1 and 2 of the snout. Note the bimodal distribution of *V. l. groenlandicus*.

Patterns of incisive, maxillary, and zygomatic crimping created by lateral PC2 and 3 vary considerably among all subspecies, but *V. v. fulva* tends to be nearer to the mean while those Alaskan foxes who do not also fall in the average range form three loose clusters of PC2:PC3 values (Figure 12).

Most foxes have jaws with average depth (Figure 13). Curve, captured by PC2, is most frequently shallow in red foxes, especially *V. v. fulva*, which over all has

the most variable jaw form. Narrow jaws are also most common in *V. vulpes*, but a few have thick, straight jaws (Figure 14).

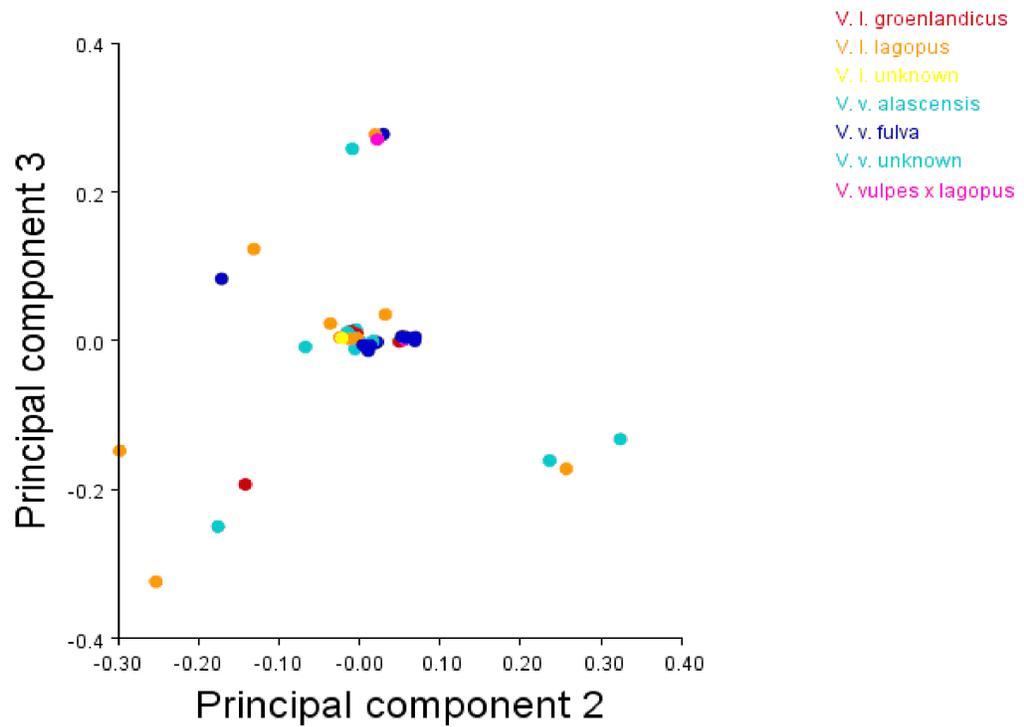


Figure 12. PC2 and 3 for the snout. PC3 is correlated to sex ($p = 0.002632$).

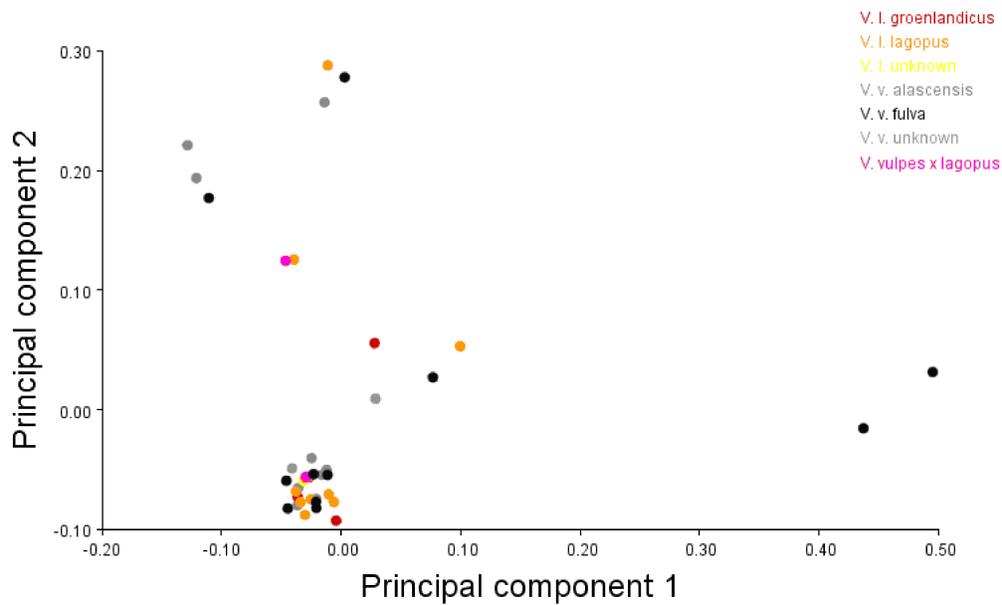


Figure 13. Values for principal components 1 and 2 of the jaw.

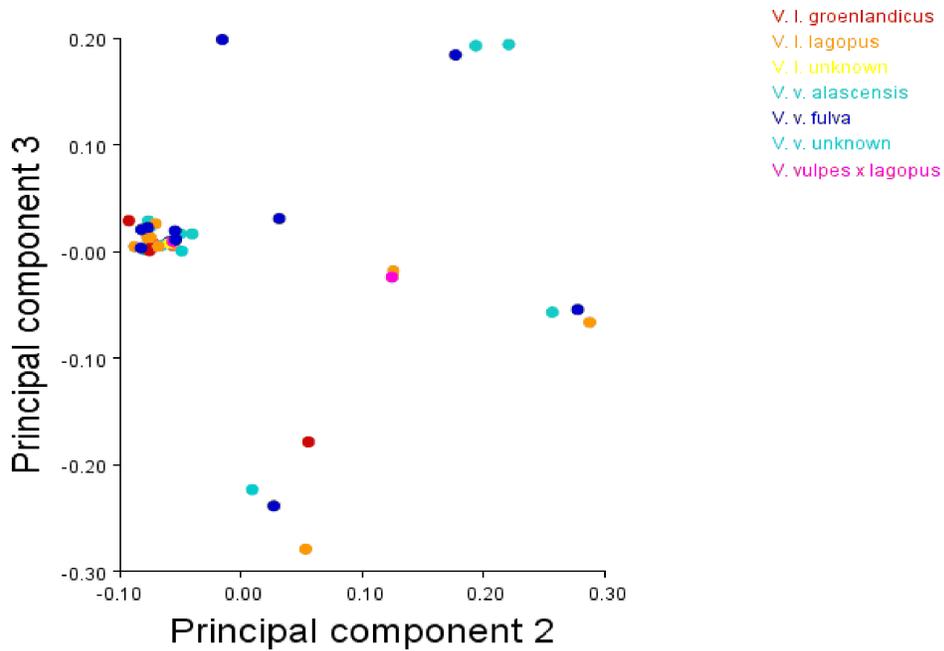


Figure 14. Principal components 2 and 3 of the jaw. *V. v. fulva* displays high levels of variation.

Trends by Sex and Size

Males are more likely to have jaws that do not narrow anteriorly than females, and to express a degree of crimping that changes the angle at the roots of their emerging canines. Otherwise, no sex related trends stand out.

No significant relationships between any shape changes and size were found, except for Ventral PC3. Larger individuals tend to have a broader muzzle with a stronger bend in the molar row.

Statistics

Out of 48 comparisons, MANOVA found four statistically significant correlations between subspecies, sex, or size and over all or specific PC for each set of physical features. Correlations were found between subspecies and the width of the zygomatic arches (dorsal PC3), between size and over-all muzzle compaction, between size and ventral PC3, and between sex and the set of the upper canines (lateral PC3). No other statistically significant correlations between subspecies, sex, size, and any over all or specific shape variables were found (Table 3).

Correlation of Shape to Subspecies Expressed by <i>p</i> Values				
	Overall	PC1	PC2	PC3
Sagittal Crest	2.3769	0.6863	0.1412	2.26e-06
Palate	0.5741	0.1306	0.6371	0.7982
Snout	0.7652	0.4845	0.9393	0.4232
Jaw	0.8288	0.4364	0.8496	0.6701
Correlation of Shape to Sex Expressed by <i>p</i> Values				

	Overall	PC1	PC2	PC3
Sagittal Crest	0.6823	0.4817	0.7553	0.4363
Palate	0.4318	0.08397	0.9706	0.4699
Snout	0.0557	0.7247	0.7078	0.00263
Jaw	0.8142	0.4847	0.9702	0.492
Correlation of Shape to Size Expressed by <i>p</i> Values				
	Overall	PC1	PC2	PC3
Sagittal Crest	0.43	0.7498	0.2197	0.1198
Palate	0.02336	0.04755	0.0893	0.5397
Snout	0.9834	0.8542	0.9732	0.7084
Jaw	0.2508	0.2606	0.6942	0.1032

Table 3. Correlation of shape to subspecies, sex, and size as expressed by *p* values generated by MANOVA. Of 48 tests, only four yielded statistically significant correlation ($p < 0.05$).

DISCUSSION

Variation in *V. v. fulva* and *V. l. groenlandicus*

Shape variation data confirms that *V. v. fulva* is a highly polymorphic subspecies of red fox. Given the variability of its habit across the northeastern United States and Atlantic Seaboard, if it endeavors to take advantage of the wide variety of habitats found in its range it must not confine itself to a single niche (Ables 1975). A high degree of variation in skull shape, and thus diet, competition ability, and temperature tolerance makes this possible. Skull shape varies even between members of the same population of *V. v. fulva*. Besides average skull types, both paedomorphic, *V. l. groenlandicus*-like and paramorphic, *V. v. alascensis*-like skull types are seen in *V. v. fulva*, as are variations seen in no other subspecies tested. This is reflective of the temperatures *V. v. fulva* living in different regions must cope with; some *V. v. fulva* encounter long winters, while others live in comparatively balmy climates. Depending on their home range, their diet may be the ancestral meadow hunter's fare of small rodents and berries, or the suburban fox's preferred fare stolen garbage and livestock. Competition may be significant or minor (Hersteinsson and MacDonald 1992). Thus, for every fox, the best solution differs. The paedomorphic type offers superior protection against cold, and is not limiting when a wide range of foods is available and only low competition is present. The paramorphic type is useful for foxes on a more meat based diet or in areas with high competition as it emphasizes jaw strength.

The average type permits variation in dietary routine and copes well enough with moderate cold and competition. For all of these variations to exist in the same subspecies, a flexible skull shape is required. This flexibility may be due to developmental plasticity, and the range of types expressed if so is indicative of responses to local conditions during development. The variety of responses present in even the small sample size studied here highlights how plastic red foxes can be. Compared to the other subspecies examined, their adaptability is unparalleled.

V. l. groenlandicus contrasts with *V. v. fulva* in that its skull shape is fairly close to a fixed type. There is some degree of variation in skull slope and jaw shape. Though minor compared to the amount of variation found in *V. v. fulva*, this comes as a surprise, as it was thought Arctic foxes lacked visible variation within subspecies (Szuma 2008). The basic features Arctic foxes are said to be predisposed to – small broad muzzles, rounded skulls with small sagittal crests and compensating deep jaws – are confirmed, however, in this subspecies' morphology (Fraçkowiak et al. 2013). This likely relates to the lack of competition with other small carnivores *V. l. groenlandicus* enjoys. As the only fox on the island, and the only small carnivore besides the ermine, this fox does not need to worry about same-sized competitors besides conspecifics (Bennike et al. 1989). Thus, it is simply built to resist the weather and handle its diet, and this is reflected in its skull. Its snout is short and broad, and its skull is domed. Its

profile is often beaked instead of sloped, which is likely a side effect of the paedomorphosis that shortens the muzzle and domes the skull (fig). This particular shape decreases heat loss from the head and reduces the risk of frost bite in the nose, which is beneficial in their climate. Their tendency for a weak sagittal crest is also likely a consequence of paedomorphosis, but it is compensated for with a sturdy jaw and in some individuals, a mid-dorsal section of the crest still develops into a pronounced ridge (fig). This is likely due to maturation of the crest which results from regular use of the temporalis muscles, as only that section of the crest increases in size (Liem et al. 2001). The rest of the skull in individuals with better developed crests is not otherwise too differently shaped than the skulls of Greenland Arctic foxes with mean or low values for sagittal crest shape. Wide zygomatic arches are also typical in *V. l. groenlandicus*, which may imply larger masseters, which would also increase bite force in a compensating manner (Liem et al. 2001). This, apparently, serves them well enough on small prey like lemmings, baby birds, and carrion.

Variation in Alaskan Foxes

Results for shape variation in *V. v. alascensis* were not entirely unexpected. As predicted, shape differences between Alaskan red foxes did not come down entirely to sexual dimorphism. Only one trait was statistically linked to sex (Table 3). This corresponds to a difference in dentition noted previously in red foxes, in which males tend to have a different shape than females (Szuma 2008). This

study's findings confirm the validity of this dimorphism and open the possibility of it extending to other species. However, other features of their skulls were found to differ not simply due to sex or size. Taken together, the combined differences in shape among *V. v. alascensis* compared to other foxes point to a paramorphic development of the sagittal crest at the expense of maintaining the compact snout more typical of foxes. While a large sagittal crest can be achieved in any individual due to regular use of the temporalis, the development of a strong sagittal crest over time in later in life does not secondarily elongate the muzzle, as the rest of the skull is no longer responding to changes across its entirety (Liem et al. 2001). Thus, it is more likely that *V. v. alascensis* acquire their well developed crests early in their ontogeny and due to the constraints of growth fields during that time, continue growing the anterior half of their skull as well as the posterior, even though that is not adaptive (Davis 1964). Individuals able to develop prominent sagittal crests early in life are better able to take advantage of the primarily meat-based calorie sources Alaska offers. Superior bite force, of course, is also an advantage in offensive interactions as well (Valkenburgh et al. 2002). If, as some anecdotes suggest, red foxes regularly prey on arctic foxes, then these benefits overlap (Pamperin et al. 2006). Depending on how far north Alaskan red foxes with elongated snouts venture north, or into high altitude, their muzzles will be no greater disadvantage to them in the cold than their large bodies, long legs, and relatively big ears are already, so this feature may be more non-adaptive than

mal-adaptive (Hersteinsson and MacDonald 1992). They could certainly continue to thrive where they currently reside, and expand further north if temperatures rise enough to accommodate their size. However, not all Alaskan red foxes bear elongate muzzles. Others have more moderate muzzles and crests. These foxes, depending on if they can respond to selective pressure to develop smaller size, may be able to push further north. Given the comparatively small size some Nearctic-derived subspecies on the east coast achieve, perhaps Holarctic red foxes in the north west can adapt as well, especially if these two clades are crossing where their ranges overlap. While it is hardly as variable as *V. v. fulva*, *V. v. alascensis* is a little more variable than expected, and certainly more variable than *V. l. groenlandicus*, and the future of their evolution is open-ended. Surprisingly, though, *V. l. lagopus* nearly matches its level of shape variation.

V. l. lagopus was expected to show conserved morphology like *V. l. groenlandicus*. However, just as *V. l. groenlandicus* was found to separate into clusters for a few morphological traits, so does *V. l. lagopus*. The angles at which their zygomatic arches and teeth are oriented vary, as does the slope of their forehead. Bowing of the arches and maxilla and bulbous heads are associated with the rounding and shortening of features produced by paedomorphosis, and the degree of paedomorphosis expressed may explain the variation of these features in this subspecies, as well as the others in which these features are found. Skull type in some members of this subspecies are more paramorphic than paedomorphic,

however. As in *V. v. alascensis*, there exist two clusters of individuals of both sexes who have less compact muzzles than most (fig). This may hinder those individual's cold tolerance a small degree, but, if it is a consequence of assimilation of acquired characteristics such as a more developed sagittal crest, as it seems to be in *V. v. alascensis*, then it may be worth the loss, especially in warmer parts of their range. The Alaskan Arctic fox already employs a deep jaw and wide zygomatic arches to make the most of its diet. A large sagittal crest and a correspondingly large temporalis muscles could further increase their fitness for hypercarnivory, and perhaps allow them to better hold their own in territorial disputes. As some *V. l. lagopus* do have both fairly well developed sagittal crests and elongated muzzles, this may very well be the case.

The Arms Race

The shape variations seen in Alaskan red and Arctic fox palates – and thus, muzzles – are the same in both subspecies. Members of both groups have either average muzzles, moderately elongate muzzles, or muzzles which are quite elongate, based on principal component values and the shape changes associated with those values (Figure 3). This suggests both species are responding to similar pressures to improve bite force. They must experience either lack of pressure to maintain muzzle shape, in which case muzzle shape is non-adaptive, or the pressure to improve bite force outweighs the pressure to maintain a compact muzzle, in which case an elongate muzzle is maladaptive, but worth working

around. If this shape is indeed adaptive, since both species exhibit it, then it is too early to say the Arctic fox is failing to compete with the red fox. Both species produce this phenotype, and in the southern parts of Alaska where the minimum temperature is not so extreme, the less compact muzzle it causes is not a burden.

It is thus possible that given time, the Alaskan Arctic fox could evolve to more evenly match the Alaskan red fox. Clearly, the population can produce a similar skull shape. The population can also produce a large size, as is evident from the long, bulky skulls seen in captive bred *V. l. lagopus*, which achieve their size because of a rich diet and selective breeding. Large, wild Arctic foxes living in portions of their range where size and an elongate skull are not disadvantageous, such as warmer, more urban areas with stable year food sources, could eventually evolve to the size of their captive descendants if that phenotype proves as successful for them as it has for *V. v. alascensis*. The long-muzzled, strong-crested members represented in this study may be the seeds from which this hypothetical type develops. Given that a large Arctic fox stands a better chance of holding its own against a red fox, selective pressure on size and strength likely exist, and given that *V. l. lagopus* has more variability to draw on than expected, this path of evolution is not impossible for the subspecies, and may be its salvation.

However, *V. v. alascensis* may adapt more quickly, given the red fox' higher plasticity. It may be that *V. l. lagopus* with the phenotypic variations witnessed already existed by the time *V. vulpes* reentered the Northwest, and that *V. v.*

alascensis has adapted to match it. *V. v. alascensis* may also be able to adapt to mirror the phenotype of the Arctic foxes which survive in the extreme North of their range, by shrinking their body size and evolving the paedomorphic features present in Arctic foxes. Members of *V. v. fulva*, after all, express some of these traits. The genes and methods of altering development present in these Nearctic foxes may be present in the Holarctic foxes as well. If so, the Alaskan red foxes with paramorphic features may not be the ones to ultimately extirpate the Arctic fox; it may be those who respond to the pressure of the Arctic to become metabolically conservative. Either way, the demands of the environment and the competition between the two species will push both species to change. The Alaskan red fox could continue to move towards a conserved, hypermorphic phenotype and remain bound in the south, or evolve to cope better with the restraints on size found farther north, or the Arctic fox could increase its size and strength to compete with the red fox in its southern range. The red fox may be able to adapt at a faster rate, but given the unexpected amount of variability found in the Arctic fox, they may be able to keep pace for longer than previously expected. One could succeed in displacing the other, but if they adapt at similar rates, they may stay as they are, locked in a stalemate.

The benefits of variability are why the lack of statistically significant correlation between subspecies and shape variations in this study are encouraging, not disheartening. Animals with a chance to evolve and keep up with ever-

changing environments must be variable. When compared against one another, plastic animals living in diverse habitats, like foxes, should resist clustering, because environmental factors should cause variation between individuals. Should *V. v. fulva*, for example, have had a single, obvious phenotype correlated with it, that would imply the once-variable subspecies had become limited in its diet, or temperature tolerance, and thus unable to utilize as much of the available habitat and resources its range offers, or had been out-competed in all but one of the niches it occupied. But, *V. v. fulva* is incredibly variable, and *V. v. alascensis*, *V. l. groenlandicus*, and *V. l. lagopus* are all also variable to different degrees, indicating they are responding to environmental factors in healthy ways. For the Arctic foxes, this is particularly good news, as global warming is changing their habitat at a more rapid rate than they have formerly experienced. They may be able to tap into their variability and plasticity to change in time to survive.

Of course, lack of correlation may also be due to small sample size, or variables unaccounted for. The skull, for all it can convey, is a limited subject. Individual range data, competition levels, and accurate dietary information like what can be gathered from gut content is absent, and at best can be inferred. Studies on living, monitored fox populations would offer better insight into what, if anything, accounts the most for the different phenotypes seen in sympatric and allopatric red and Arctic fox populations.

For now, the state of fox populations in Alaska remains unsettled. Alaskan red

foxes have moved towards a more conserved skull shape than *V. v. fulva* exhibits, but that phenotype may offer both dietary and behavioral advantages as it promotes bite strength. However, it may be disadvantageous in extreme cold, and restrict *V. v. alascensis* from some parts of *V. l. lagopus*' range. *V. l. lagopus* exhibits similar phenotypes, implying they are responding to similar pressure with the same developmental response. As Arctic foxes were thought to lack the variation and adaptability of red foxes, this is an encouraging result. In the changing landscape of the Arctic Circle, any avenue its iconic species have to adapt provides hope for the species' continued existence.

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