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Paleozoological Data Suggest Euroamerican Settlement Did Not Displace Ursids and North American Elk from Lowlands to Highlands

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Abstract The hypothesis that Euroamerican settlement displaced some populations of large mammal taxa from lowland plains habitats to previously unoccupied highland mountain habitats was commonly believed in the late nineteenth and early twentieth centuries. By the middle twentieth century biologists had come to favor the hypothesis that Euroamerican colonization resulted in the extirpation of populations of large mammal in lowland habitats and those taxa survived in pre-existing relict populations in the highlands. Why modern biologists changed their minds is unclear. There is no historical evidence that unequivocally favors one hypothesis over the other. The low-elevation Columbia Basin of eastern Washington state in the northwestern United States is surrounded by forested mountains. The majority of historical records (1850 AD or younger) of black bear (*Ursus americanus*), brown bear (*Ursus arctos*), and North American elk (*Cervus elaphus*) occur in mountainous, coniferous forest habitats. Paleozoological records of these taxa $\leq$ 10,000 year old and >160 year old in both highland and lowland habitats suggest the displacement hypothesis does not apply to ursids and elk in this area. These taxa seem to have been more or less ubiquitous in the area prior to Euroamerican colonization (ca. 1850 AD), and were extirpated from lowland habitats after colonization. Recent colonization of lowland shrub-steppe habitats by elk in particular, although historically unprecedented, must be categorized as recolonization rather than an invasion. Whether a species is classified as indigenous or nonindigenous may influence management activities focused on that species. The paleozoological record indicates ursids and elk are indigenous to the highland forest habitats of eastern Washington.

Keywords Biogeographic displacement · Eastern Washington State · Extirpation · North American elk Paleozoology · Ursids

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Introduction

Beginning in the late nineteenth century, some North American biologists came to believe that taxa of large mammals had been displaced from their native lowland ranges as a result of settlement of those ranges by Euroamerican colonists. One of the most vocal of those biologists was George Bird Grinnell who as early as 1894 argued that large game species "until killed or driven off [had been] abundant in rough bad land country far from the mountains [of Montana and Colorado]" (Grinnell 1894, p. 312). He repeated this biogeographic hypothesis for more than thirty years, arguing that the displaced species had previously been numerous in lowland habitats of the plains and prairies when undisturbed by humans but they had retreated to, and come to take up residence in, highland mountain habitats when in danger (e.g., Grinnell 1928). I refer to this notion hereafter as the lowland-to-highland displacement hypothesis.

The lowland-to-highland displacement hypothesis was repeated by a number of biologists during the late nineteenth and early twentieth centuries, and concerned several species of large mammal (Elliot 1899; Fryxell 1926; Huntington 1904; Skinner 1927). Perhaps the most noteworthy discussion of this hypothesis was Rush's (1932, p. 26) summation of the 1881 through 1928 annual reports

of the Superintendent of Yellowstone National Park on large game (particularly elk), and his conclusion that "the Park area was not originally heavily stocked with game animals" but had only recently become so (see also Graves 1917; Grimm 1939). Empirical support for the displacement hypothesis was the fact that the mountains were unsuitable for large populations of game animals as evidenced by the fact that many individuals starved there in the winter (Rush 1932).

Skinner (1927) provided a very detailed discussion of the lowland-to-highland displacement hypothesis, and included historical observations and ecological data to validate his belief that it accurately described the biogeographic history of at least some large mammals. Skinner (1927, p. 169) noted that "large animals" were abundant and occurred in large aggregates on the "wide open prairies and plains when pioneers first entered the west." The same species occurred in the mountains but were represented by considerably fewer individuals, probably, Skinner suggested, because the mountains did not contain sufficient forage. Skinner devoted four pages to summarizing the wildlife observations of nineteenth century explorers of the Yellowstone country, pointing out that as a whole, the men in those parties reported a paucity of game in the highlands. He then argued that this began to change about 1880 with the "last great killing on the plains," after which it seemed likely that the surviving animals took refuge in the mountains (Skinner 1927, pp. 175–176). Carnivores such as ursids and canids followed the game animals—ungulates—into the mountains.

The lowland-to-highland displacement hypothesis began to loose favor in the early twentieth century, though a few individuals at the time still thought it valid (Ingles 1965; Larrison 1967; Murie 1951; O'Connor 1961). It is difficult to pinpoint when the lowland-to-highland displacement hypothesis began to loose favor, but Adolph Murie (1940) has been credited with setting the record straight and arguing that the idea that ungulates in particular had once been rare in highland mountain habitats relative to their abundance on lowland plains was erroneous (Buechner 1960). Murie (1940, p. 2) suggested Grinnell (e.g., 1894, 1928), Skinner (1927), Rush (1932), and others, were largely responsible for perpetuating the idea that in the "early days game was scarce in the mountains; that it is much more abundant there now than it was originally; that game [dispersed] to the mountains about 1880; and that game [had previously been] more abundant on the plains than in the mountains." He presented a number of reasons that this false impression might be thought true, including the fact that many taxa migrated to the highlands in the summer yet explorers tended to move through low elevation areas; there was heavy predation along heavily traveled routes so large game would have been scarce in those areas; large game animals were much more visible on the level, grassy plains than in the topographically complex and heavily forested mountains; and finally, some mountain habitats were poor in game naturally.

The alternative to the lowland-to-highland displacement hypothesis that replaced it can be labeled the lowland-extirpation-highland-relict hypothesis. It had been discussed throughout the twentieth century (Armstrong 1972; Bailey 1931; Hoffmann and Pattie 1968; Meagher 1973; Peek 1982; Pelton 2000; Zeveloff and Collett 1988). Late in the twentieth century Bryant and Maser (1982, p. 23) indicated there "is a general verbal consensus among contemporary biologists that hunting pressure and settlement did not push the herds of elk into the more rugged, inaccessible regions, but rather that herds in 'competition' for the land to be settled were simply exterminated." Why the lowland-extirpation-highland-relict hypothesis came to be favored over the lowland-to-highland displacement hypothesis is unclear. Murie's (1940) arguments for favoring the former hypothesis seem sound, but so too do Skinner's (1927) reasons for favoring the latter hypothesis. Recent interpretations of the same historical documents that Murie and Skinner consulted suggest to some that elk were rare in Yellowstone National Park prior to its establishment (Kay 1990), and suggest to others that elk and other large game species were abundant (Schullery and Whittlesey 1992). Thus historical data cannot be used to determine which hypothesis is more likely correct.

Resolving which of the two alternative hypotheses applies to a particular highland-occupying species is pertinent to deciding whether that species is indigenous or non-indigenous to an area. Insofar as that decision influences how species are managed (Donlan and Martin 2004; Lodge and Shrader-Frechette 2003, 2004), knowing which hypothesis holds is critically important. Conservation and wildlife management actions and decisions must be based on the best available empirical evidence rather than folklore, hearsay, or tradition (Sutherland and others 2004). Schullery (1997, p. 47) suggested that "study of the archaeological and paleontological record should help" choose between the lowland-to-highland displacement hypothesis and the lowland-extirpation-highland-relict hypothesis. I take some initial steps toward testing these two hypotheses here, referring to archaeological and paleontological faunal remains as paleozoological materials.

Study Area

I use the eastern half of Washington state as the geographic area for testing the hypotheses. The eastern portion of Washington is topographically a basin, with the drainage outlet of the Columbia River in the southwestern corner

(Fig. 1). The central area is known as the Columbia Basin and is bordered on the north and west by the Columbia River, and on the south by the Snake River, a major tributary to the Columbia. The Columbia Basin is relatively low in terms of elevation and is dominated by shrub–steppe habitats (Daubenmire 1970; Franklin and Dyrness 1973). Mountains encircle the Columbia Basin—the Cascade Range on the west, the Okanogan Highlands on the north, the Selkirks and various portions of the Rockies on the east, the Blue Mountains on the southeast, and the Ochoco Plateau on the southwest (McKee 1972). The mountains support coniferous forests of varied taxonomic composition (Franklin and Dyrness 1973). Virtually all early Euroamerican settlers who came to eastern Washington in the mid nineteenth century homesteaded in the Columbia Basin (Dryden 1968); few settled in the mountains except in the bottom of deep canyons (Marsh 2004). Together, topography and settlement history make eastern Washington an ideal study area for testing the lowland-to-highland displacement hypothesis. If large mammals were resident in the low-lying Columbia Basin prior to Euroamerican settlement, land modification practices, particularly those related to agriculture, could have displaced those resident species to higher elevations or merely extirpated resident lowland populations, leaving highland populations less influenced if influenced at all. Here I use the lower elevational limit of coniferous forests as the boundary between highland (forested) and lowland (shrub-steppe) habitats.

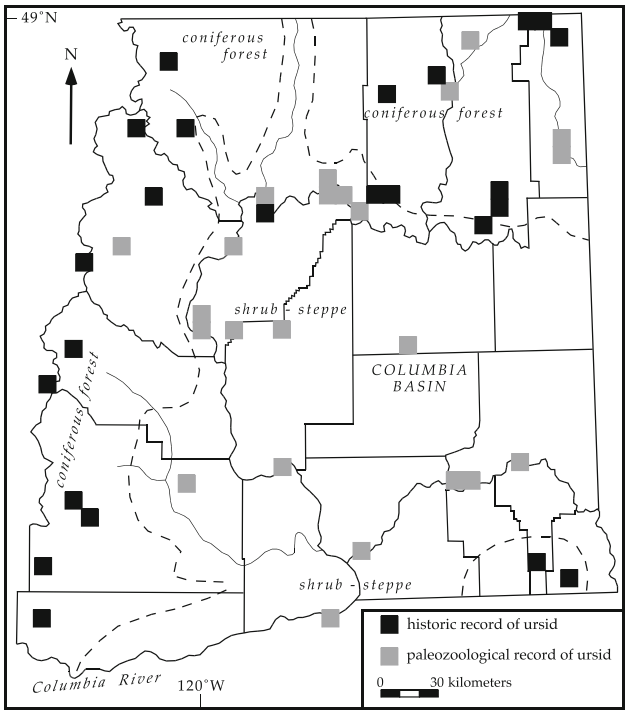

Fig. 1 Historic (post-1850 AD) and paleozoological (pre-1850 AD to 10,000 BP) records of ursids (*U. americanus, U. arctos*) in eastern Washington state. Each square is a Township (9.6 × 9.6 km) and may contain more than one record. *Dashed line* marks the boundary between lowland shrub-steppe habitats and highland forest habitats. *County lines* are shown for reference

Methods and Materials

To test the two hypotheses, I use two mammalian taxa, both of which today occur in mountainous, forested habitats. Ursids, both black bear (*Ursus americanus*) and brown bear (*U. arctos*), were chosen because they are often in some form of competition with humans. Thus, they would have perhaps been perceived by human colonists as pests to be removed, whether exterminated or displaced (Pasitschniak-Arts and Messier 2000; Pelton 2000). Both species are included in analyses here because many reported ursid remains from paleozoological contexts are identified only to genus. The second taxon chosen is the North American elk (*Cervus elaphus*). It is a popular game species that, in the Pacific Northwest, was nearly exterminated early in the twentieth century (Wisdom and Cook 2000).

I consulted the FAUNMAP database (Graham and Lundelius Graham and others 1994), and supplemented the paleozoological records listed there by examining all written archaeological and paleontological reports known to me concerning the Holocene paleozoology of eastern Washington. County lines that follow or approximate the east–west drainage defined by the crest of the Cascade Range serve as the western boundary (Fig. 1). I recorded the number of identified specimens (NISP) (Grayson 1984; Lyman 2008b) of ursid and elk remains recovered from each archaeological site and paleontological location when such data were reported; sometimes only the presence of remains was reported. A specimen is a bone or tooth or fragment thereof. Only those archaeological remains that were not modified into artifacts were recorded to avoid including bones and teeth that had been transported long distances from where animals were procured (Lyman 1994); I know of no paleontological remains of elk or ursids that are of Holocene (last 10,000 year) age, so none were recorded for this study.

The age of remains was determined using stratigraphically associated radiocarbon ages, temporally diagnostic artifacts that were stratigraphically associated in the absence of the radiometric ages, or temporally distinct strata such as radiometrically dated volcanic tephra (e.g., Lyman 2000a). Geographic locations of deposits that produced remains of ursids and elk were recorded by official state archaeological site number, and by legal description (township, range). All locations where ursid or elk remains have been recovered were mapped by township (9.6 × 9.6 km), which makes the prehistoric data

comparable to the historic data (see below). Each unique township that has produced remains of ursids and of elk is noted regardless of how many locations or sites within that township have produced remains.

Because sampling of eastern-Washington deposits that contain mammalian remains has not been probabilistic (random) or systematic across geographic space (Lohse and Sprague 1998; Lyman 2002), efforts to determine the prehistoric range of ursids and elk, or to monitor changes in the distribution of ursids and elk, must be tempered by knowledge that the samples may not be representative of the total geographic area or the various portions of it under consideration. The presence of remains of ursids and elk that are unlikely to have been transported by human agents or natural processes is taken as evidence of relatively local origin (<10 km away from the recovery location). The absence of remains of either taxon may reflect local absence, lack of preservation of remains, or lack of recovery of remains as a result of sampling error (Grayson 1981; Lyman 1994, 2002, 2004b).

In eastern Washington, the older a deposit, the less intensively and extensively it has been sampled (Ames and others Ames and others 1998; Lyman 2000a, b, 2004a). Prehistoric changes in the abundance of elk remains over time are of ambiguous significance because the apparent temporal trends depend on how data are aggregated (Lyman 2010b). Too few ursid remains are known to seek trends in relative abundance of this taxon over time. Particular ages of individual faunal remains from paleozoological contexts are, however, irrelevant to simple determination of whether ursids and elk were displaced upward topographically by Euroamericans. Thus, here I distinguish only between those remains that are pre-1850 AD and those that are younger than 1850 AD.

Historic occurrence records of ursids and elk were taken from Johnson and Cassidy (1997) and from Booth (1947). Locations reported by Booth (1947) were of less spatial resolution than those presented by Johnson and Cassidy (1997), but were plotted to the closest township. Johnson and Cassidy (1997) confirmed records they report by visual inspection of curated specimens collected between 1818 and 1995. It is reasonable to suspect that the majority of these specimens were collected after 1850 as this is when most mammal surveys were done; for example, of the 19 surveys listed by Hall (1932) that took place between 1820 and 1930, only three pre-date 1850. Not only does the date of 1850 AD approximate the age of the earliest historic records on local mammalian biogeography (Taylor and Shaw 1929; Hall 1932; Booth 1947; Dalquest 1948), it also marks more or less sufficient post-initial Euroamerican settlement for displacement and local extirpation to have occurred.

Evaluation of the association of ursids and elk with highland and lowland habitats at particular times (pre- and post-1850 AD) involves presence of known-age remains of these taxa in those settings. It cannot be concluded that the absence of remains of a species indicates that the taxon was not present in the area; remains may not have been found for any of several reasons (Lyman 2008a). I use 2×2 contingency tables to determine whether a taxon is significantly associated with a particular habitat at a particular time.

Hypotheses and Predictions

There are several possible biogeographic histories of mammals in eastern Washington. One is the lowland-to-highland displacement hypothesis; another is the lowland-extirpation-highland-relict hypothesis. As phrased in the Introduction, these are mutually exclusive and have anthropogenic causes. It is possible, however, that a combination of the two is what actually took place. That is, some lowland populations may have been extirpated while others were displaced. And it is also possible that environmental change was a contributory cause of shifts in the ranges of ursids and elk about 150 years ago. In particular, the so-called "Little Ice Age" extended from about 1300 to 1850 AD (Mann 2002). This climatic interval may have caused elk in particular to migrate from higher to lower elevations during winter months, a phenomenon known among some modern elk (Irwin 2002), or to colonize lower elevations and remain there year-round as a result of too cool summers. Paleozoological data indicate that elk were present in the Columbia Basin through out the Holocene (last 10,000 years), both before and during the Little Ice Age as well as during other climatic extremes, both warm and cool (Lyman 2004b). It is unclear if elk were only present seasonally (during the summer), but this is irrelevant to the two main hypotheses. Available evidence suggests the beginning of the Little Ice Age did not cause elk to start migrating to, or to stay in the lowland habitats of the Columbia Basin during summer months because they were present there (perhaps only seasonally, perhaps year round) before that climatic interval.

It is difficult to determine from archaeological faunal remains if humans exterminated populations of prey animals (Grayson and Meltzer 2002), though it is possible to find evidence of depression (not necessarily depletion) or decreased availability of those populations to predators (Grayson 2001). In that regard, there is no clear evidence that human hunters of the last 200 years or so did, or did not, depress lowland Columbia Basin populations of elk and ursids. The evidence that prehistoric (pre-1800 AD) hunters may have depressed the elk population is ambiguous (Kay 1994; Lyman 2004a, 2010b; Lyman and Wolverton 2002; Martin and Szuter 1999). I therefore here

simply assess the two main hypotheses described in the introduction. Once these have been evaluated, we will have a better idea of what actually happened and, if appropriate data can be generated, then the other hypotheses described above can be assessed.

The lowland-to-highland displacement hypothesis presumes that individuals of the displaced lowland taxa were not present in significant numbers, if at all, in the highlands prior to the displacement of lowland populations. Predictions of the lowland-to-highland displacement hypothesis in terms of paleozoological remains can therefore be stated as follows: First, remains of displaced species found in highland sites should be no older than 1850 AD; second, remains of displaced species in lowland sites can be of any age, but not significantly or often younger than 1850 AD. Predictions of the lowland-extirpation-highland-relict hypothesis are as follows: First, remains of species from highland sites can be of any age, historic or prehistoric; second, remains of extirpated species in lowland sites should date prior to 1850 AD but not younger than that. The second prediction is the same for both hypotheses, so the diagnostic prediction is the first one alone. Note, however, if individuals of displaced taxa were present in the highlands prior to displacement of lowland populations, the first prediction of the lowland-to-highland displacement hypothesis becomes identical to the first prediction of the lowland-extirpation-highland-relict hypothesis. In such a case, a paleozoologically based choice between the two hypotheses could not be made.

Results

As of late 2009, 30 archaeological sites have produced remains of ursids, including six sites that have produced remains of brown bear, a species extirpated in the state for nearly a century (Lyman 1986). All ursid paleozoological remains predate 1850 AD. The 23 geographic townships in which the sites are located are plotted in Fig. 1 (more than one paleozoological site occurs in some townships). Also plotted in that figure are the historically known (post-1850 AD) records of black bear and brown bear. Twenty-one of the 24 townships (87 percent) with historical records (post-1850) of ursids are located in highland forest habitats (Table 1); 18 of 23 townships (78%) with paleozoological records and 20 of the 30 paleozoological sites (67%) with paleozoological records of ursids are from lowland shrub-steppe habitats (Fig. 1). Regarding the distribution of townships with historical and prehistoric records of ursids, there is a significant association between the age of ursids (pre- or post-1850 AD) and their elevation or habitat (lowland shrub-steppe or highland forest) ($\chi^2 = 17.97$; $P < 0.0001$).

As of late 2009, 96 archaeological sites have produced remains of elk. Those sites all predate 1850 AD and are distributed across 61 townships. The 61 geographic townships in which the sites are located are plotted in Fig. 2 (more than one paleozoological site occurs in some townships). Also plotted in that figure are the historically known records of elk. Twenty-five of the 36 townships (69%) with historical records (post-1850) of elk are located in highland forest habitats (Table 1); 54 of 61 townships (88%) with paleozoological records and 87 of the 96 paleozoological sites (91%) with paleozoological records of elk are from lowland shrub-steppe habitats (Fig. 2). Regarding the distribution of townships with historical and prehistoric records of elk, there is a significant association between the age of elk remains (pre- or post-date 1850 AD) and their elevation or habitat (lowland shrub-steppe or highland forest) ($\chi^2 = 31.84$, $P < .0001$).

Discussion

Sixty years ago Dalquest (1948, p. 172) reported that "black bear occurs in a variety of habitats in Washington. It seems to be absent only from the treeless areas of eastern Washington." At the same time, Booth (1947, p. 489) stated that "bears were once abundant in the state of Washington, but now are scarce in most regions except in the wilder areas of the Cascades, Olympic Mountains, and Blue Mountains." These observations combined with the distribution data in Fig. 1 suggest that post-Euroamerican colonization and its attendant influences on local ecosystems (e.g., hunting, agriculture) extirpated ursids from the warm dry Columbia Basin. The lowland-extirpation-highland-relict hypothesis accounts for both the historic data and the paleozoological data. The displacement hypothesis is refuted because there are prehistoric records of ursids in upland forested habitats, both in the western part of the study area and especially in the northeastern portion.

The paleozoological data for elk indicate this large ungulate was present in the forested highlands prehistorically, refuting the lowland-to-highland displacement hypothesis. The historical records indicate that elk were quickly extirpated from the Columbia Basin, likely early in

Table 1 Frequency of townships producing historic (post-1850 AD) and prehistoric (pre-1850 AD) remains of ursids and of elk in lowland shrub-steppe habitats and in highland forest habitats

	Lowland shrub-steppe	Highland forest
Ursid, historic	3	21
Ursid, prehistoric	18	5
Elk, historic	11	25
Elk, prehistoric	54	7

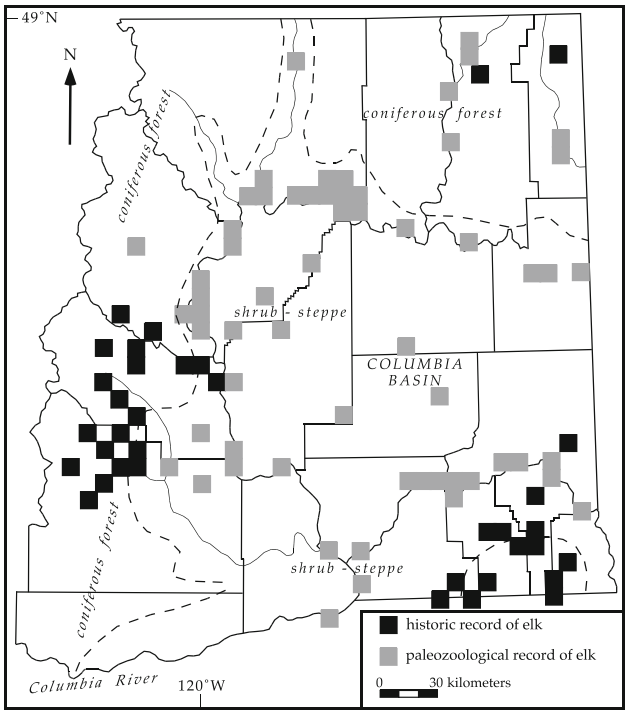

Fig. 2 Historic (post-1850 AD) and paleozoological (pre-1850 AD to 10,000 BP) records of North American elk (*Cervus elaphus*) in eastern Washington state. Each square is a Township (9.6 × 9.6 km) and may contain more than one record. *Dashed line* marks the boundary between lowland shrub-steppe habitats and highland forest habitats. *County lines* are shown for reference

the nineteenth century. Booth (1947, p. 571), for example, reported that the elk "likely ranged formerly over most of the eastern portion of the state, but then was exterminated." Dalquest (1948, p. 391) agreed and stated that "lumbering, agriculture and settlement as well as excessive hunting removed [the elk] from parts of eastern Washington… Only in the [state's mountains] did the elk survive in appreciable numbers." As with the ursids, the weight of the evidence, both historical and paleozoological, favors the lowland-extirpation-highland-relict hypothesis for elk. Given the paucity of archaeological research done in the highland forest habitats of eastern Washington, and the plethora of such research done in the lowland shrub-steppe habitats there (Lyman 2002), future research will likely reveal many remains of ursids and elk in both kinds of habitats dating prior to 1850 AD, but remains in the highlands in particular will strengthen the validity of the lowland-extirpation-highland relict hypothesis.

Conclusion

The lowland-to-highland-displacement hypothesis may have arisen because mountains tend to be remote relative to industrial-age settlement and typically are among the last places visited by colonists who are agriculturalists. Knowledge of what might be in those places in terms of plants, animals, geological resources, and the like is initially based more on hearsay and anecdotal evidence than systematically gathered data. Knowledge of what is not there is equally speculative. Elk and ursids were rarely observed in the lowlands at the time of initial colonization, perhaps because populations were to some degree depleted by American Indian hunters (Lyman 2004a), and it is clear that they could not be found there after 1900. Elk in particular could occasionally be found in the mountains prior to 1900 but were becoming increasingly rare (Elliot 1899; Edson 1916; Dice 1919; Taylor and Shaw 1927; Macy 1934), prompting transplanting from Yellowstone herds (Couch 1935). Given that it may have been unclear if elk and ursids occurred in forested highlands in presettlement time, it is not a stretch to suggest that Euroamerican colonists inferred that they, themselves, displaced these quadrupeds into new habitats, just like the colonists themselves were moving into new habitats (and displacing American Indians). Without explicit and unambiguous historical records of elk and ursids in the mountains prior to colonization and settlement, the lowland-to-highland displacement hypothesis nicely fit what was known, particularly when it was observed that numerous individuals of the supposedly displaced taxa starved to death when they spent the winter in the mountains. Paleozoological data in the case of ursids and elk suggest that the lowland-extirpation-highland-relic hypothesis is more likely than the displacement hypothesis in eastern Washington. What is the relevance of this observation for conservation biology and wildlife management?

In 1977 the first historically authentic record of elk colonizing the shrub-steppe habitats of eastern Washington was reported (Rickard and others 1977). This was such an unprecedented and unexpected event that the three-paragraph report focused on the fact that the colonized area was an "isolated" and "protectively managed reserve" that had not been subjected to agriculture-related land modification (Rickard and others 1977, p. 1009). It apparently was thought that these characteristics, plus abundant forage, had allowed the colonization. Although it is difficult to dispute this interpretation, paleozoological data indicate that the 1977 colonization event was not a seminal colonization event nor was it an instance of invasion; rather it was a recolonization event (Lyman 2004b).

The case studies presented here indicate that knowing which hypothesis of historical biogeography is supported in a particular case will be important when it comes to categorizing species on the basis of their biogeographic histories and founding conservation and restoration actions on those categorizations. For example, in contrast to elk recolonizing the shrub-steppe habitats of eastern

Washington, there is no paleozoological evidence to suggest that the recently documented colonization by moose (*Alces alces*) of eastern Washington is a recolonization event. Rather, it seems to be a result of a growing and geographically expanding population of moose in central Idaho (Lyman 2010a). That may have a bearing on how the resident Washington moose are managed. If they are categorized as nonindigenous and invasive and they become traffic hazards or pests, then appropriate management action can be taken (presuming no paleozoological evidence of their presence in the past is found in the interim).

The lowland-to-highland displacement hypothesis and the lowland-extirpation-highland-relict hypothesis concern the difference between local population movement or relocation and local population extirpation, respectively. Which hypothesis holds for individual taxa in a particular area will likely vary from instance to instance given the individualistic hypothesis of biogeography (Whittaker 1970) and whether or not local anthropogenic processes affected a taxon's distribution. It has become clear that empirical evidence from the historic period may be insufficient in scope or detail (e.g., Randklev and others 2010); until my study, this was the case with respect to the lowland-to-highland displacement hypothesis and the lowland-extirpation-highland-relict hypothesis. Thus Schullery (1997) is correct to suggest that the prehistoric record provided by zooarchaeological and paleontological remains may help resolve particular conservation issues (see also Lyman 2006). With respect to ursids and elk in eastern Washington, it is now clear that their histories best conform to the lowland-extirpation-highland relict hypothesis rather than the lowland-to-highland displacement hypothesis; these taxa are indigenous to the highland forest habitats of eastern Washington. Management choices can now be made with this knowledge firmly, that is, empirically, in hand.

Acknowledgments The lowland-to-highland displacement hypothesis is one that my father, a lifetime resident of southeastern Washington, believed and taught me, especially with respect to the local elk population. Despite his inaccuracy, I miss him and here gratefully acknowledge that had he not taught me what he did, I would not be doing what I do today and having so much fun doing it. Thanks to B. Akersten, C. Randklev, S. Wolverton, and several anonymous reviewers for comments on an early draft.

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