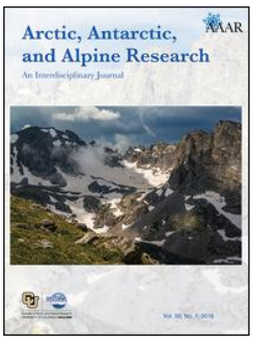

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SIGNIFICANCE FOR WILDLIFE MANAGEMENT OF THE LATE QUATERNARY BIOGEOGRAPHY OF MOUNTAIN GOATS (*OREAMNOS AMERICANUS*) IN THE PACIFIC NORTHWEST, U.S.A.

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ABSTRACT

Management policy of the U.S. National Park Service regarding mountain goats (*Oreamnos americanus*) in Olympic National Park, Washington, is founded in part on the argument that alpine environments there evolved through the late Quaternary without mountain goats. Descendants of mountain goats artificially introduced to park lands in the 1920s are being experimentally sterilized and translocated to control population size. The potential that *Oreamnos* sp. colonized and inhabited the Olympic Mountains during the late Quaternary is, however, great. Prehistoric and historic extralimital records of mountain goats in Oregon and northern California, the Wisconsin glacial and floral histories, and the modern distributions of other alpine and subalpine mammalian taxa suggest the Puget lowland served as a biogeographic filter rather than a barrier for mammalian taxa during periods of maximum glacial extent. Extirpation of isolated mountain goat populations on mountains of Oregon, California, and Washington apparently took place throughout the Holocene. Future documentation of the prehistoric occurrence of *Oreamnos* sp. in the Olympic Mountains should prompt rethinking of National Park Service wildlife management policy.

INTRODUCTION

Wildlife management involves adopting policies and making decisions regarding a complex publicly owned resource (Bailey, 1982). Management objectives tend to be directed towards insuring or enhancing benefits to be realized in the future as well as maintenance and enhancement of present benefits (Langenau and Ostrom, 1984). Because policies and decisions are based on available data, management will only be as good as those data, particularly in the long term. Thus, concerted effort to obtain all available data bearing on a policy or decision should be made. In this paper I illustrate the significance of the prehistoric faunal record for making well-informed management decisions and the potential fallacies that may become built-in to management policies if that record is ignored.

There is presently some concern over management of the mountain goat (*Oreamnos americanus*) in Olympic National Park of western Washington (Figure 1). This taxon was artificially introduced in the 1920s to what were to become park lands in 1938 (Moorhead and Stevens, 1982). In following years, the population grew from the original dozen to 1100 to 1200 which now occupy some 1800 km^2 (Houston et al., 1986). The occupied area receives relatively less rain and snow than other portions of the Park, and perhaps because of this, mountain goats have not dispersed from the major mountain complex to which they were originally introduced (Moorhead and Stevens, 1982; National Park Service [NPS], 1981). The population is near estimated carrying capacity and over the past decade has seriously impacted plant communities by trampling and grazing (NPS, 1981, 1982, 1983, 1984).

Arguments to remove mountain goats in order to preserve the alpine floral and geological ecosystems are founded on the conclusion that the alpine ecosystems evolved without mountain goats. Moorhead and Stevens (1982) follow Scheffer (1946) and Dalquest (1948) and suggest that some alpine and boreal mammals native to Washington's Cascade Range were biogeographically isolated from the Olympic Mountains by the intervening Puget Sound and Puget lowland. For example, Dalquest (1948: 61) suggests that the upper elevations of the Olympics are effectively a biogeographic island when he notes "the Olympic Mountains rise above the timberline and are surrounded by forested lowlands which in a sense isolates this mountain range."

The possibility that the Puget lowland acted as a barrier to the dispersal of mammalian taxa is an issue separate from the evidence used to conclude that mountain goats are not native to the Olympic Peninsula. I first consider the evidence for the conclusion. Then, the potential for dispersal of mammals from the Cascade Mountains of Washington across the Puget lowland to the Olympic Mountains is evaluated.

THE EVIDENCE

The evidence which Moorhead and Stevens (1982) believe indicates that *Oreamnos americanus* is not native to the Olympics consists of three parts: a lack of historic reports of mountain goats by biologists, a lack of ethnographic reports of native mountain goats, and a lack of prehistoric evidence of native mountain goats. I consider each in turn.

Moorhead and Stevens's (1982) review of historic biologic surveys fails to describe the geographic areas surveyed. While several surveys were made around the perimeter of the Olympic Mountains over 100 yr ago (Table 1, Figure 1), none of these appears to have actually covered large areas of modern mountain goat range. Therefore, mountain goats might not have been recorded because appropriate areas were not surveyed.

Moorhead and Stevens (1982: 47) report that "in the isolated Olympic Mountains no early faunal remains or ethnographic evidence of mountain goats have been reported." Bergland (1983: 16) suggests "the dearth of anthropological information for the interior portion of the Olympic National Park is the result of (1) lack of accessibility, (2) dense vegetation and rugged terrain, (3) the belief that aboriginal inhabitants of the Olympic Peninsula did not make appreciable use of the mountains, (4) lack of scholarly interest, and (5) lack of funding." Similarly, some biologists have suggested "mountain goats were not greatly exploited by Indians and early settlers because of the inaccessibility and remoteness of their habitat" (Wigal and Coggins, 1982: 1017; see also Grant, 1905). Other biologists (e.g., R. L. Johnson, 1977, 1983) cite historic records of Indians hunting mountain goats in the northern Cascades of Washington (Brooks, 1930). Ethnographic and ethnohistoric data indicate Indians of British Columbia actively pursued mountain goats for their wool, flesh, and horns (Gunther, 1972). Cultural differences in subsistence activities may account for the lack of ethnographic evidence indicating Olympic Peninsula Indians hunted this alpine mammal (e.g., Singh, 1966). Ethnographic data may thus be poor indicators of the presence or absence of native *Oreamnos americanus* in the Olympic Mountains.

Archaeological research on the Olympic Peninsula has been focused on near-coast sites (Figure 1). This research has produced faunal remains, but thus far none has been identified as *Oreamnos* sp. Such remains may not have yet been found because so few sites have been studied (Figure 1), the sites are located some distance from mountain goat habitat, most of the sites had relatively small volumes of sediment examined, and the samples of recovered mammal bones are small (see overviews in Bergland, 1983; Wessen, 1983). If recovered from these sites, remains of *Oreamnos* sp. may not have been recognized as such. In summary, the archaeofaunal record for the Olympic Peninsula may not be representative of the Holocene mammalian fauna that lived there, and thus may be a poor indicator of the presence or absence of mammalian, especially alpine, taxa.

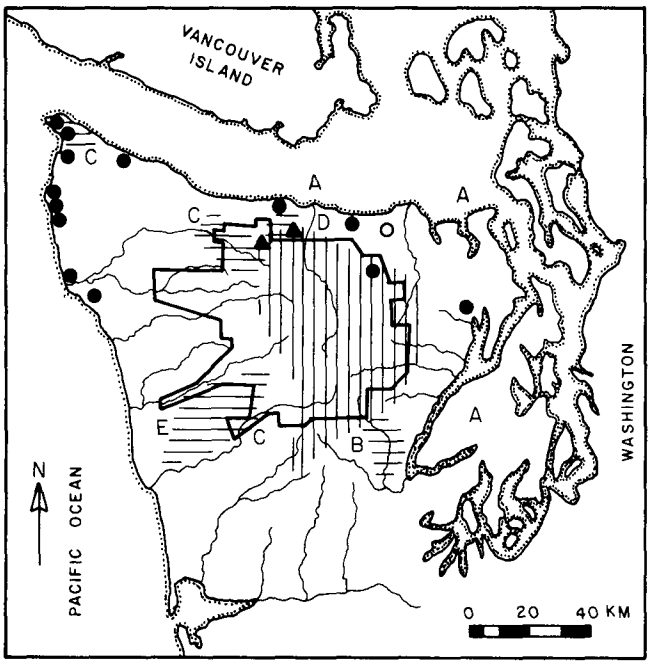

FIGURE 1. Olympic Peninsula of western Washington. Olympic National Park is outlined with heavy line (coastal portion of Park not shown). Vertical cross-hatching indicates present range of mountain goats; triangles are 1920s goat release sites. Horizontal cross-hatching and capital letters indicate 19th and early 20th century biological survey areas (see Table 1 for key). Dots are locations of studied archaeological sites; circle is the Manis Mastodon Site.

TABLE 1
Biological expeditions to the Olympic Peninsula[a]

Date	Expedition	Area visited (Figure 1 location)
1841	U.S. Exploring Expedition	From Straits of Juan de Fuca and Puget Sound to interior (A)
1894	Clark P. Streator (U.S.D.A.)	Lake Cushman (B)
1897	U.S.D.A. Biological Survey	Headwaters of Solduc River, Lake Quinault, Neah Bay (C)
1898	Field Museum of Natural History	Lake Southerland, Crescent Lake, Happy Lake, Elwah River (D)
1917–1921	U.S.D.A. Biological Survey	Various, into mountains
1919	University of Michigan, Walker Expedition	Lake Cushman (B)
1931	Cleveland Museum Expedition	Quinault/Queets divide, Hoh River (E)

[a]After Hall (1932).

There is no paleontological evidence of native mountain goats in the Olympic Peninsula because no Quaternary fossil localities have been studied in this region (Kurtén and Anderson, 1980; Lundelius et al., 1983; Harris, 1985). Such localities may in fact be rare, as Harington (1971: 1081) notes "remains of alpine species undergo particularly heavy erosion in fast-running streams and consequently are seldom preserved." The absence of paleontological remains of *Oreamnos* sp. in the Olympic Mountains therefore cannot be used as evidence to argue that native mountain goats were not at one time extant in the area.

The conclusion that mountain goats are not native to the Olympic Peninsula is based on negative evidence. It is tenuous to argue a species was not present in an area even when fossil localities and archaeological sites in that area have been examined (Grayson, 1981). To argue a species was not present without having truly looked for it is even more tenuous. It is equally tenuous to state, as Lundelius et al. (1983: 344) do, that "the late Pleistocene faunas of the Olympic Peninsula were similar to those of the Rocky Mountains to the east; the mountainous parts of both regions shared taxa such as *Oreamnos americanus*." There is no evidence to support such a statement. The most reasonable position is to hypothesize mountain goats were present in the Olympic Mountains during the late Quaternary. This hypothesis requires that the route and timing of dispersal be modeled. The model should also account for the apparent early twentieth-century absence of mountain goats from the Olympic Mountains.

TABLE 2
Boreal mammalian taxa historically absent from the Olympic Mountains and present in the Cascade Mountains of Washington[a]

Ovis canadensis[b] (D, J)
Ochotona princeps (D, J)
Spermophilus lateralis (J)
Lynx canadensis (J)
Ursus arctos[b] (J)

[a]Reported by Dalquest (D) (1948) and Johnson and Johnson (J) (1952).
[b]Taxa whose ranges diminished in eastern Washington during the Holocene (Lyman, 1986b; Lyman and Livingston, 1983).

THE PUGET LOWLAND AS A DISPERSAL ROUTE

The Puget lowland is held responsible for the absence of several species from the Olympic Mountains, species which are present in the Cascade Mountains (Table 2). Of these taxa, Johnson and Johnson (1952: 37) wrote "there is no indication, past or present, suggesting that these species ever inhabited the Olympics, though the requirements for their existence would seem to be prevalent here."

The late Quaternary (last 20,000 yr) biogeographic history of mammalian taxa in eastern Washington has been dynamic (Lyman and Livingston, 1983; Lyman, 1986a, 1986b), and the late Quaternary biogeographic history of western Washington has also been dynamic. Remains of bison (*Bison* sp.) and caribou (*Rangifer* sp.) dating between 12,000 and 9000 BP have been recovered from the Manis Mastodon site in the northeast corner of the Olympic Peninsula (Petersen et al., 1983; Figure 1), yet neither of these taxa was reported in the 19th and early 20th century biological surveys of this area.

ENVIRONMENTAL FACTORS

Dalquest (1948) suggested that boreal and alpine mammals of the Olympics originated in the Mount Rainier area and moved westward across the outwash of Cascade alpine glaciers and the Cordilleran ice sheet to the outwash of Olympic glaciers, and that the environment through which these taxa dispersed was like an alpine meadow. In the 35 yr since Dalquest outlined his hypothe-

sis of a Puget lowland biogeographic route, we have learned much about the late Quaternary environmental history of western Washington. There are two aspects of this history which are relevant to modeling the Puget lowland as a biogeographic route: glaciers and vegetation.

Northern areas of Washington, Idaho, and western Montana were covered with the Cordilleran ice sheet 15,000 ± 1000 yr ago (Figure 2). This ice sheet was retreating from northeastern Washington and northern Idaho by 13,000 BP. The Puget lobe of this ice sheet reached its southern limit about 14,250 ± 250 BP, and shortly afterward began to recede. By 13,600 BP its southern terminus had reached the northern Puget lowland (Waitt and Thorson, 1983). Alpine glaciers occupied many of the higher altitude areas of Washington, Oregon, and Idaho during the late Pleistocene (Figure 2). Most of these in the Cascades "had retreated at the time of the culminating advance of the Puget lobe. In many valleys west of the Cascade crest, lakes were ponded between thick ice in the Puget lowland and the Cascade alpine glaciers" (Porter et al., 1983: 84). The Olympic Mountains alpine glaciers advanced and retreated prior to 18,000 BP (Waitt and Thorson, 1983).

On one hand, much of the Washington Cascades today inhabited by mountain goats and other alpine mammals was unavailable for occupation between approximately 17,500 and 13,500 BP (compare Figures 2 and 3). Alpine habitats of the Olympic Mountains, on the other hand, would have been available for occupation during this period as this area was relatively ice free after 18,000 BP.

Palynological data indicate that between 17,000 and 12,500 BP, the area between Puget Sound and the Cascade crest contained a vegetational gradient; treeless conditions prevailed in the north, pine-parkland in mid-latitude areas, and forests in the south. Dominant vegetation in the mid-latitude areas consisted of pine (*Pinus* sp.), spruce (*Picea* sp.), mountain hemlock (*Tsuga mertensiana*), and herbs (Heusser, 1983). In the Puget lowland tundra-parkland vegetation prevailed between 19,000 and 17,000 BP and changed to spruce-pine parkland between 17,000 and 15,000 BP. From 15,000 to 12,500 BP, spruce–mountain hemlock parkland prevailed, suggest-

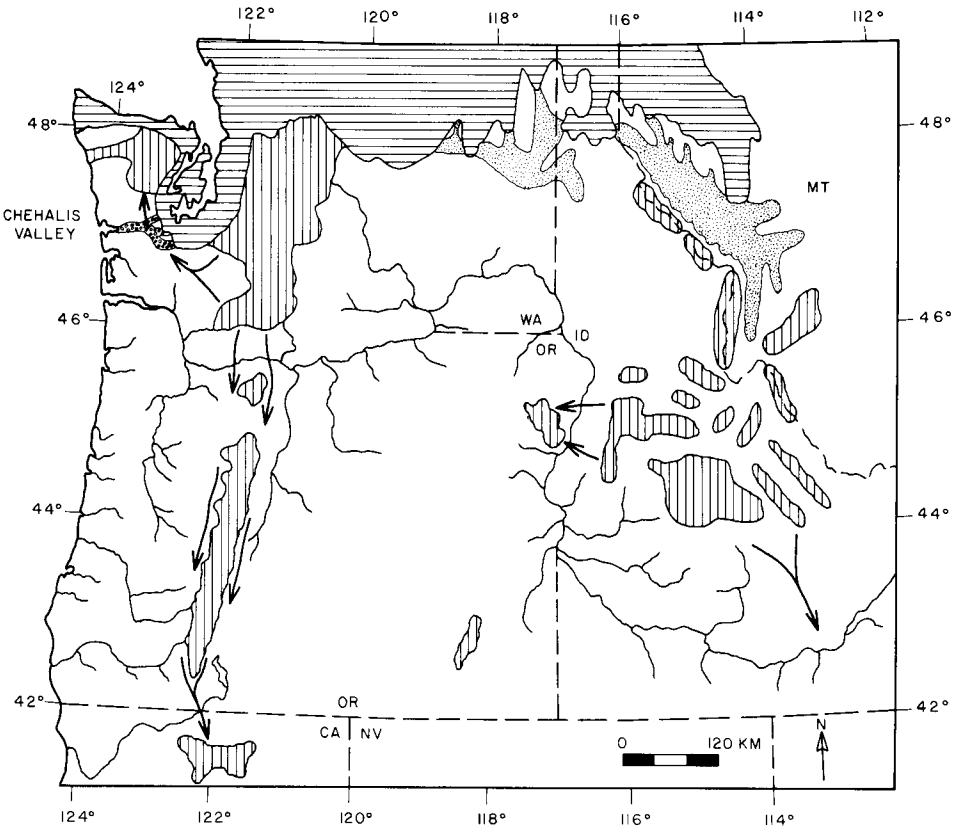

FIGURE 2. Extent of glaciers ca. 15,000 BP (incomplete for western Montana). Cordilleran ice sheet indicated by horizontal cross-hatching (after Waitt and Thorson, 1983); alpine glaciers indicated by vertical cross-hatching (after Porter et al., 1983); stipling indicates glacial lakes (after Waitt and Thorson, 1983). Note that alpine glaciers in the Olympic Mountains would not be present, having receded by 18,000 BP. Chehalis Valley glacial outwash plain indicated as draining west from the Puget Lobe of the Cordilleran ice sheet. Heavy arrows indicate the hypothesized dispersal routes of mountain goats. Compare with Figure 3.

ing maritime climatic conditions. The southern Puget lowland experienced a relatively continental climate between 19,000 and 17,000 BP as evidenced by pollen of xerophytic taxa. The climate became more mesic and maritime-like after 17,000 BP and especially so by 15,000 BP (Barnosky, 1984). Due to the rain shadow effect of the Olympic Mountains and the (inferred) more southerly position of winter storm tracks, the eastern slopes of the Olympic Mountains contained at least some open herb-and-shrub dominated communities between at least 12,000 and 11,000 BP (Petersen et al., 1983), and perhaps earlier.

Given the apparent ecological predilections and food habits of *Oreamnos americanus* (Campbell and Johnson, 1983, and references therein), between 17,500 and 13,000 BP the Puget lowland and contiguous unglaciated areas provided suitable (if not optimal) habitat for this taxon. The suitability of this area may have been enhanced by the glacial omission of more optimal high-altitude habitats. Harington (1971: 1091) suggests that periods of maximum glaciation during the Pleistocene eastward dispersal of ancestral *Oreamnos* sp. across Beringia forced the animals "to survive on the lower grasslands," and that "an analogy between winter-summer and glacial-interglacial mountain goat habitat is relevant." Studies of extant mountain goats indicate some populations utilize different summer and winter ranges, particularly when winters are harsh. Summer ranges are found at higher elevations than winter ranges when the latter have minimal south exposure and/or minimal cliff-area from which snow is removed by wind. Seasonal variation in diet concomitant with shifts in ranges has also been documented (e.g., Hebert and Turnbull, 1977; Smith, 1977). During the Wisconsin glaciation the relatively snow- and ice-free eastern slopes of the Olympics may have been quite attractive to immigrating mountain goat populations.

Dalquest (1948) speculated that prior to the last Wisconsin glacial advance (prior to 18,000 BP) *Oreamnos americanus* occupied an extensive range in Washington. When the last advance occurred (17,500 to 13,500 BP), mountain goats were confined to the southern Cascades. *Oreamnos americanus,* Dalquest (1948: 109) wrote,

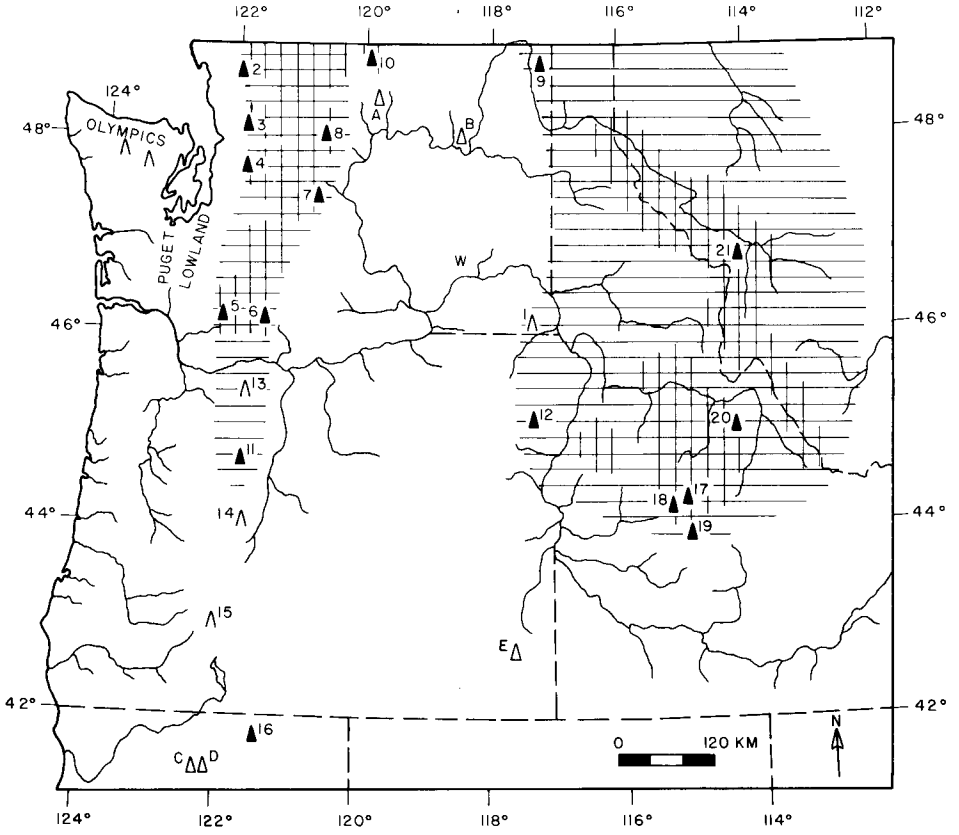

FIGURE 3. Modern distribution of mountain goats in the Pacific Northwest. Horizontal cross-hatching is distribution shown by Hall (1981); vertical cross-hatching is distribution shown by Johnson (1977; see also Wigal and Coggins, 1982). Filled triangles are historic records of mountain goat occurrences; triangles with closed base are prehistoric records of *Oreamnos* sp.; triangles without base are locations conjectured to have prehistoric and early historic records of mountain goats on the basis of the dispersal model outlined in the text (see Table 3 for key to number and letter code).

"seems not to have crossed the Columbia River to become established in the Cascades of Oregon." After ice retreat (ca. 13,500 BP), mountain goats dispersed northward through the Cascades of Washington and back into British Columbia, according to Dalquest's (1948) hypothesis.

The Puget lowland may have been suboptimal mountain goat habitat during the period of maximum glacial extent, but the palynological data indicate forage requisite for nutritional survival was available (Hebert and Turnbull, 1977, and references therein). The major obstacle along the dispersal route between the southern Cascades and the Olympic Mountains may have been the glacial outwash plain of the Chehalis River valley (Figure 2). The fact that this potential barrier was apparently crossed at some unknown time in the past by the yellow pine chipmunk (*Tamias amoenus*), a species found at both ends of the route but not in intervening areas today (Hall, 1981), indicates Chehalis Valley and the Puget lowland may have acted more as a filter to small mammals than as a barrier to their biogeographic dispersal. The filtering effect on large mammals may have been of an even lesser magnitude.

Pacific Northwest Mountain Goat Historic Biogeography

Several different maps of the modern distribution of *Oreamnos americanus* have been published (R. L. Johnson, 1977, 1983; Hall, 1981; Wigal and Coggins, 1982). Two of these distributions are shown in Figure 3. Only one published map shows mountain goat range in Oregon (Hall, 1981), but this is not Bailey's (1936) map, despite an earlier report of two occurrences of mountain goats in that state (Grant, 1905). As well, a single report of an early 19th century occurrence of this species in northern California (D. R. Johnson, 1970) is not cited by any recent survey. It is unclear why some of these records (e.g., Grant, 1905) are treated differently by various biologists while other records (e.g., D. R. Johnson, 1961, 1970) are not considered at all.

R. L. Johnson (1977, 1983) tends to epitomize the perspective most modern biologists have of the prehistoric biogeography of mountain goats in the Pacific Northwest.

> While extinct species of *Oreamnos* may have ranged from Yukon Territory to California, the current distribution of mountain goats is similar to historical occurrence. A fossil mountain goat recovered from Lake Washtucna in eastern Washington indicates the environmental conditions or habitat requirements of mountain goats have changed considerably since their invasion during the Pleistocene era [R. L. Johnson, 1983: 2].

While this statement begs the question of when the historic period began, it is more significant that the Lake Washtuckna fossil specimen is not *Oreamnos* sp., but rather part of a mastodon (*Mammut* sp.) tooth (Fry and Gustafson, 1974; Harington, 1971). (The town near the fossil locality is spelled "Washtucna"; the lake's name was apparently spelled "Washtuckna" at the time the fossil in question was discovered.)

Five sites in the Pacific northwest have produced prehistoric remains of *Oreamnos* (Table 3, Figure 3). Two are near Mount Shasta in northern California; the remains are Rancholabrean in age (Sinclair, 1904, 1905; Furlong, 1906; Harington, 1971) and of an unknown species of *Oreamnos* (Harington, 1971; Mead, 1983). Two other sites are located in north-central Washington; the remains date to the last 3000 yr and apparently represent *O. americanus* (Collier et al., 1942; Grabert, 1974). The fifth site reported to contain remains of *Oreamnos* is located in southeastern Oregon; based on associated artifact styles the remains appear to date to the last 2000 yr but the species represented is unknown (Hubbard, 1967). All five prehistoric records are extralimital relative to the present-day distribution of this taxon (Figure 3).

The Chopaka Mountain population of mountain goats (Figure 3) immigrated to this area "about 1910 from a resident population north of the border in British Columbia" (R. L. Johnson, 1983: 4), and has undergone drastic reduction since 1940 for some, as yet, unknown reasons (Campbell and Johnson, 1983). This population is geographically close to the archaeological record at Coulee Creek Rockshelter (Figure 3). These facts suggest small populations of mountain goats may have occasionally immigrated into regions more or less adjacent to their more usual range throughout the Holocene, only to die or move out of this new region within a century or two. If the modern range of *O. americanus* is controlled by environmental factors, perhaps fluctuations in range borders are indicative of past environmental fluctuations. Regardless of that possibility, it is clear that minor fluctuations in biogeographic range are experienced by *Oreamnos,* and this may account for some of the variation in the two range maps in Figure 3.

Dispersal Model

To account for the prehistoric and early historic extralimital records of mountain goats involves minor modifications to Dalquest's (1948) hypothesis. I conjecture that prior to 18,000 BP, *O. americanus* occupied the Washington Cascades and the northern Rocky Mountains of Idaho and western Montana. Between 17,500 and 13,500 BP, they occupied the southern mountain ranges of Idaho, and dispersed westward to the Wallowa Mountains of northeastern Oregon in search of suitable habitat, perhaps as a response to overcrowding in the mid-latitudes of Idaho's mountain ranges. Similarly, mountain goat populations in Washington's southern Cascades were overcrowded, and as a response dispersed southward across the Columbia River (when it was frozen over?) to the Oregon Cascades, eventually coming to occupy the flanks of Mount Hood, Mount Jefferson, the Three Sisters, Mount Mazama, and Mount Shasta in California. Some also dispersed westward from Washington's southern Cascades across the Puget lowland and then northward to the Olympic Mountains. After 13,500 BP areas

previously occupied by glacial ice were inhabited by mountain goat populations which more or less followed the retreating Cordilleran ice sheet northward.

Mead (1983) suggests that *O. americanus* and *O. harringtoni* diverged from a common ancestor that had dispersed throughout much of the mountainous western United States during the last 100,000 yr. He did not consider the possible dispersal of *Oreamnos* to the Olympic Peninsula as it was not germane to his model, but his suggested dispersal routes and point of origin for the mountain goats in northern California are similar to my own suggestions. If the timing of my model is correct, fossil mountain goats in northern California, Oregon, and the Olympic Mountains should be osteologically

TABLE 3
Documented and conjectured historic and prehistoric locations of mountain goats in the Pacific Northwest

Reference	Location[a] (elev. in meters)	Figure 3
Washington		
Dice (1919)	Blue Mountains (1829) [S]	1
Brooks (1930)	Mount Baker (3285) [H]	2
Dalquest (1948)	Mount Baker [H]	2
	Mount Higgins (1585) [H]	3
	Mount Index (1822) [H]	4
	Mount Saint Helens (2550) [H]	5
	Mount Adams (3742) [H]	6
	Mount Stuart (2886) [H]	7
	Lake Chelan area [H]	8
	Northeastern Washington area [H]	9
Johnson, D. R. (1961)	Sullivan Lake area (1829) [H]	9
Campbell and Johnson (1983)	Chopaka Mountain (2377) [H]	10
Matthew (1902)	Washtuckna Lake[b]	W
Grabert (1974)	Coulee Creek Rockshelter (2134) [P]	A
Collier et al. (1942)	Site 24 [P]	B
Lyman (this paper)	Olympic Mountains (2380) [C]	
Oregon		
Grant (1905)	Mount Jefferson (3199) [H]	11
	Wallowa Mountains (3040) [H]	12
Bailey (1936)	Mount Hood (3427) [S]	13
	Mount Jefferson [H]	11
	Three Sisters (3040) [S]	14
Lyman (this paper)	Mount Hood [C]	13
	Three Sisters [C]	14
	Mount Jefferson [C]	11
	Mount Mazama [C]	15
Hubbard (1967)	Rattlesnake Creek Site (1524) [P]	E
Northern California		
Sinclair (1904, 1905)	Potter Creek Cave [P]	C
Furlong (1906)	Samwell Cave [P]	D
Johnson (1970)	Lava Beds National Monument [H]	16
Idaho		
Davis (1936)	Loon Creek (2740) [H]	17
	Stanley Lake (2590) [H]	18
	Alturus Lake (2590) [H]	19
	Boulder Peak (2590) [H]	19
	Salmon River Mountains (2895) [H]	20
Western Montana		
Hall (1981)	Missoula area [H]	21

[a][S], suspected historic occurrence; [H], documented historic occurrence; [P], documented prehistoric occurrence; [C], prehistoric and/or historic occurrence conjectured on the basis of the dispersal model outlined in this paper.

[b]This specimen is now believed to represent *Mammut* and not *Oreamnos* (Fry and Gustafson, 1974).

indistinguishable from *O. americanus*. If the timing of Mead's model is more accurate, fossils in these extralimital areas should osteologically approximate the ancestor common to *O. americanus* and *O. harringtoni*. Unfortunately, we as yet do not know precisely what that common ancestor looks like.

My model of biogeographic dispesal has implications for boreal and alpine taxa other than mountain goats. The example of yellow pine chipmunks has already been mentioned, and other taxa are listed in Table 4. Again, if a taxon occurs in Washington's southern Cascades but not in the Olympic Mountains today, the distribution is often explained as resulting from the Puget lowland "barrier." For example, R. E. Johnson (1977: 15) writes "wolverines (*Gulo luscus*) have never been reported from the Olympic Peninsula and coastal areas to the south. Apparently the Puget trench has provided an effective barrier to the dispersal of this species" (see also Scheffer, 1938; Yocom, 1974). Several of the species listed in Table 4 may have, however, dispersed to the Olympic's and Oregon's Cascades more or less simultaneously with mountain goats. It seems unlikely that all of the listed taxa had such a dispersal history due to the wide range of ecological tolerances represented, but it is difficult as yet to offer more refined predictions until we better understand the biogeographical histories of these taxa in contiguous areas (e.g., Lyman and Livingston, 1983).

The model I have proposed must be subjected to testing with data from the prehistoric record. If my model is correct, *Oreamnos* remains 15,000 ± 2500 yr old should be found in the Puget lowland and Columbia River gorge (Figure 4). Remains of this taxon dating throughout the last 18,000 yr should also be found in the Olympic Mountains, Oregon Cascades, northern California, and eastern Oregon. Remains of at least some of the taxa listed in Table 4 should be found in time-space contexts similar to those hypothesized for *Oreamnos*. Discovery of any such remains would lend strong support to the hypothetical dispersal model outlined here.

Why Were Mountain Goats Historically Absent from the Olympic Mountains?

It is unclear when *O. americanus* might have become locally extirpated in northeastern Oregon and the Oregon Cascades (Figure 4). Grant's (1905) report suggests that mountain goat populations in the Wallowa Mountains and around Mount Jefferson became extinct during the 19th century, and D. R. Johnson's (1970) report suggests the mountain goat population in northern California became extinct during the mid-19th century.

I suspect that at the beginning of the Holocene some 10,000 yr ago, mountain goat populations disjunct from the southern Cascades of Washington and mountains of southern Idaho may have been isolated on or near Mount Shasta, the Wallowa Mountains, Mount Mazama, the Three Sisters, Mount Jefferson, Mount Hood, and the Olympic Mountains. These seven loci may have each represented a biogeographic "island" on which random extinction events took place during the Holocene (see Newmark, 1987, and references therein). The eruption of Mount Mazama 7000 yr ago may have extirpated the local mountain goat population. Prehistoric overkill by human hunters may have eliminated one or two other isolated populations (cf. Brooks, 1930). Climatic fluctuations dur-

Table 4
Distribution of selected boreal, subalpine, and alpine mammalian taxa in western Washington[a]

Taxon	Olympic Peninsula	Puget Lowland	Southern Cascades
Tamias amoenus	+	–	+
Phenacomys intermedius	+	–	+
Martes pennanti	+	–	+,E
Martes americana	+	–	+
Gulo luscus	–	+	+
Ochotona princeps	–	+	+,E
Spermophilus saturatus/lateralis	–	–	+
Microtus richardsoni	–	–	+
Ursus arctos	–	–	–,E
Canis lupus	+,E	+	+,E
Lynx canadensis	+,–	+,–	+,–,E
Vulpes vulpes	I	I	+
Ovis canadensis	–	–	+
Bison bison	–,P	–	–
Rangifer tarandus	–,P	–	–

[a] +, present; –, absent; E, historically present, now locally extinct; I, historically introduced; P, prehistoric record. Multiple code listings indicate difference statuses reported by different authors. Data derived from Aubry (1984), Guenther (1952), Hagmeier (1956), Hall (1981), Ingles (1965), R. E. Johnson (1977), Lyman (1986b), Maser and Storm (1970), Petersen et al. (1983), Scheffer (1938), Van Gelder (1982), and Yocum (1974).

ing the Holocene may have eliminated one or two other populations. It is not difficult, then, to suggest the hypothetical prehistoric mountain goat population of the Olympic Peninsula had become extinct prior to the early 20th century, or was so small as to have escaped detection by early biologists.

DISCUSSION AND CONCLUSION

The National Park Service position can be summarized as follows:

> Olympic National Park was established in 1938 to be managed as a natural area with the primary purpose of preserving representative natural ecosystems. In contrast to this purpose, goats in the Olympics are seen as exotic species with the capacity to alter pristine ecological relationships [NPS, 1982: 1, 1983: 2].

A dozen unique plant taxa and several dozen rare and endangered plant taxa occur in the Park. Trampling and overgrazing by mountain goats have disrupted the floral ecosystem and caused erosion of otherwise stable land surfaces (Pfitsch, 1980; Pike, 1981).

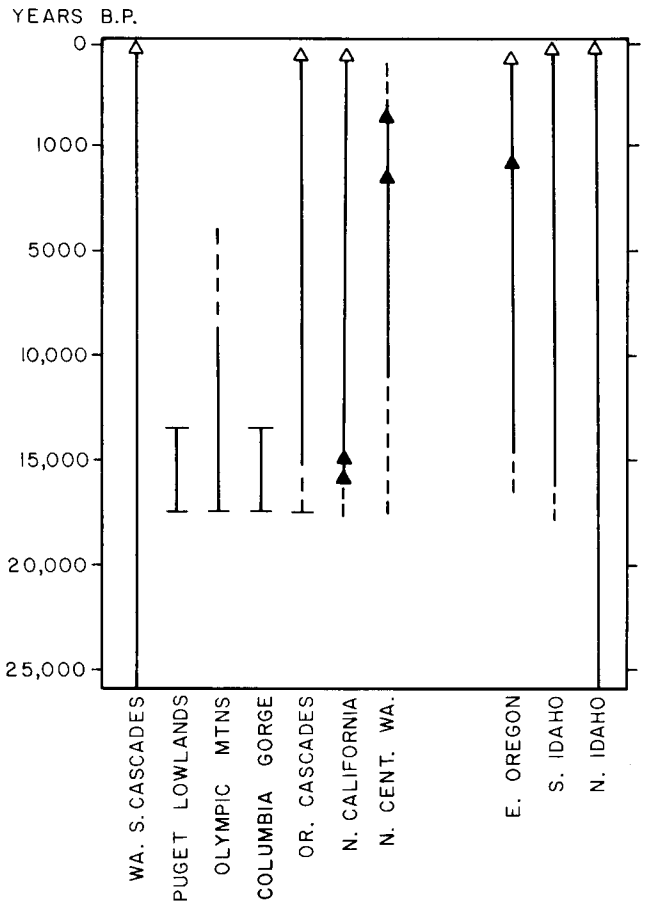

FIGURE 4. Suspected temporal occurrence of *Oreamnos* sp. in geographic areas of the Pacific Northwest if the hypothetical dispersal model is correct indicated by continuous vertical lines. Dashed vertical lines indicate terminal dates unclear; horizontal lines represent hypothesized terminal dates for occurrence; open triangles represent historic records for mountain goats; filled triangles represent prehistoric records for *Oreamnos*.

The NPS (1981: 8) argues that "plant communities in the Olympic Mountains have evolved without goats." The NPS (1981: 5) implies that mountain goats did not occur in the Olympic Mountains until they were introduced in the 1920s, and that plant communities there evolved over thousands of years without mountain goats as part of the ecosystem. National Park Service policy is "to control or remove, where feasible, exotic species that are a threat to native plants, animals and their associated communities" (NPS, 1981: 7). The NPS employs the following definitions to implement their policy:

> Exotic species are those that occur in a given place, area, or region as the result of direct or indirect, deliberate or accidental introduction of the species by humans. The native species are those which presently occur, or once did occur prior to some human influence, in a given place, area, or region as the result of ecological processes that operate and have operated without significant direct or indirect, deliberate or accidental alteration by humans [NPS, 1981: 12].

The notions of plant community evolution and natural occurrence of species at some time in the past, as expressed by the NPS, provide the important dimension of *time* to the process of making wildlife management decisions. It is no doubt because of this temporal dimension that Moorhead and Stevens (1982) attempted to demonstrate native *Oreamnos americanus* never occurred in the Olympic Mountains.

If mountain goats were every prehistorically present in the Olympic Mountains then the statement that the species is "exotic" would be false, given the definition of "native species" used by the NPS. In addition, the statement that the alpine ecosystem of the Olympics evolved without mountain goats would also be false. If this species was present prehistorically, the question then becomes one of deciding how to implement NPS policy. On one hand, given my dispersal model, it is possible that mountain goats were present in the Olympic Mountains during the late Pleistocene. This population may have died out at the end of the Pleistocene, simultaneous with the extinction of Harrington's mountain goat (*O. harringtoni*) in more southern latitudes (Mead et al., 1986). In this case it might be argued that the Holocene evolution of the Olympic ecosystem has been disrupted by the introduction of exotic mountain goats 50 yr ago. On the other hand, if this taxon dispersed to the Olympic Mountains during the late Pleistocene and became locally extirpated there during the late 18th and early 19th centuries, more or less simultaneous with its apparent extirpation in northern California, the Wallowa and Owyhee mountains of eastern Oregon, and Mount Jefferson in the Oregon Cascades, then it would be impossible to justify the position that the Olympic alpine ecosystem had been signifi-

cantly impacted by exotic mountain goats, and that this ecosystem had evolved without them.

The key to implementing NPS policy clearly lies in ascertaining the timing of mountain goat extirpation in the Olympics, and determination of the minimum age of occurrence of a taxon which makes that taxon no longer a "native." Late Pleistocene remains of mountain goats recovered from the Puget lowland would be strong circumstantial evidence for the presence of goats in the Olympics. But once such remains are found, the timing of the species' local extirpation in the Olympics becomes crucial to wildlife management decisions regarding the "exotic" population. The best possible solution, both from a purely historic zoogeography perspective and from a wildlife management perspective, is to find late Quaternary remains of this species in sites located on the Olympic Peninsula.

Would such remains, particularly if they date to the last 1000 yr, cause the NPS to reconsider its present policy regarding the modern "exotic" mountain goat population? I believe they should rethink policy issues if such remains are found. Ecological relationships are not static, but dynamic: they have evolved and are evolving regardless, in this case, of the presence or absence of mountain goats and whether those animals are descendants of native, or exotic, or a mixture of both populations of *Oreamnos*. Only detailed study of the prehistoric faunal record will clarify the "natural" status of mountain goats on Olympic National Park lands. Similar instances of wildlife management policies being solely based on historic data may have to be re-evaluated once prehistoric data are brought to bear on management issues.

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