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ARTICLE

Revised distribution of an Alaskan endemic, the Alaska Hare (*Lepus othus*), with implications for taxonomy, biogeography, and climate change

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Abstract: The Alaska Hare (*Lepus othus* Merriam 1900) is the largest lagomorph in North America but remains one of the most poorly studied terrestrial mammals on the continent. Its current distribution is restricted to western Alaska south of the Brooks Range, but historical accounts from north of the Brooks Range (the North Slope) have led to confusion over its past, present, and predicted future distributions. To determine if *L. othus* occurs or historically occurred on the North Slope, we surveyed museum collections, vetted observational accounts, and produced a spatial distribution model based on the resulting georeferenced records. We located a historic specimen long presumed lost that suggests the occurrence of *L. othus* on the North Slope as recently as the late 1800s. We also uncovered evidence of *L. othus* and (or) Mountain Hare (*Lepus timidus* Linnaeus 1758) on several islands in the Bering Sea, raising the possibility of recurring gene flow between these closely related species across seasonal ice connecting Asia and North America. While our results paint a more complete picture of the current distribution of *L. othus*, persistent uncertainties surrounding its taxonomic status and potential northward range shift onto lands reserved for oil and gas development call for additional study.

Key words: Alaska Hare, Arctic Hare, *Lepus othus*, Mountain Hare, North Slope.

Résumé : Le lièvre d'Alaska (*Lepus othus* Merriam 1900) est le plus grand lagomorphe en Amérique du Nord mais il demeure un des mammifères terrestres du continent qui n'a aiment pas fait l'objet d'études. Sa distribution actuelle est restreinte à l'ouest de l'Alaska au sud de la chaîne de Brooks, mais les récits historiques provenant du nord de la chaîne de Brooks (le versant nord de l'Alaska) ont créé une certaine confusion au sujet de ses distributions passée, présente et prédite pour le futur. Dans le but de déterminer si *L. othus* est présent ou était présent historiquement sur le versant nord de l'Alaska, nous avons étudié les collections dans les musées, vérifié les récits d'observation, et créé un modèle de la distribution spatiale fondé sur les mentions géoréférencées. Nous avons repéré un spécimen historique longtemps présumé perdu qui suggère la présence de *L. othus* sur le versant nord de l'Alaska aussi récemment que la fin du dix-neuvième siècle. Nous avons aussi trouvé la preuve de la présence de *L. othus* et (ou) du lièvre variable (*Lepus timidus* Linnaeus 1758) sur plusieurs îles dans la mer de Béring, ce qui soulève la possibilité du flux de gènes récurrent entre ces espèces étroitement liées entre la glace saisonnière reliant l'Asie et l'Amérique du Nord. Tandis que nos résultats brossent un tableau complet de la distribution

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actuelle de *L. othus*, des études supplémentaires seraient nécessaires en raison des incertitudes persistantes entourant son statut taxonomique et de son déplacement potentiel vers le nord sur des terres réservées à la mise en valeur du pétrole et du gaz.

Mots-clés : lièvre d'Alaska, lièvre arctique, *Lepus othus,* lièvre variable, versant nord de l'Alaska.

Introduction

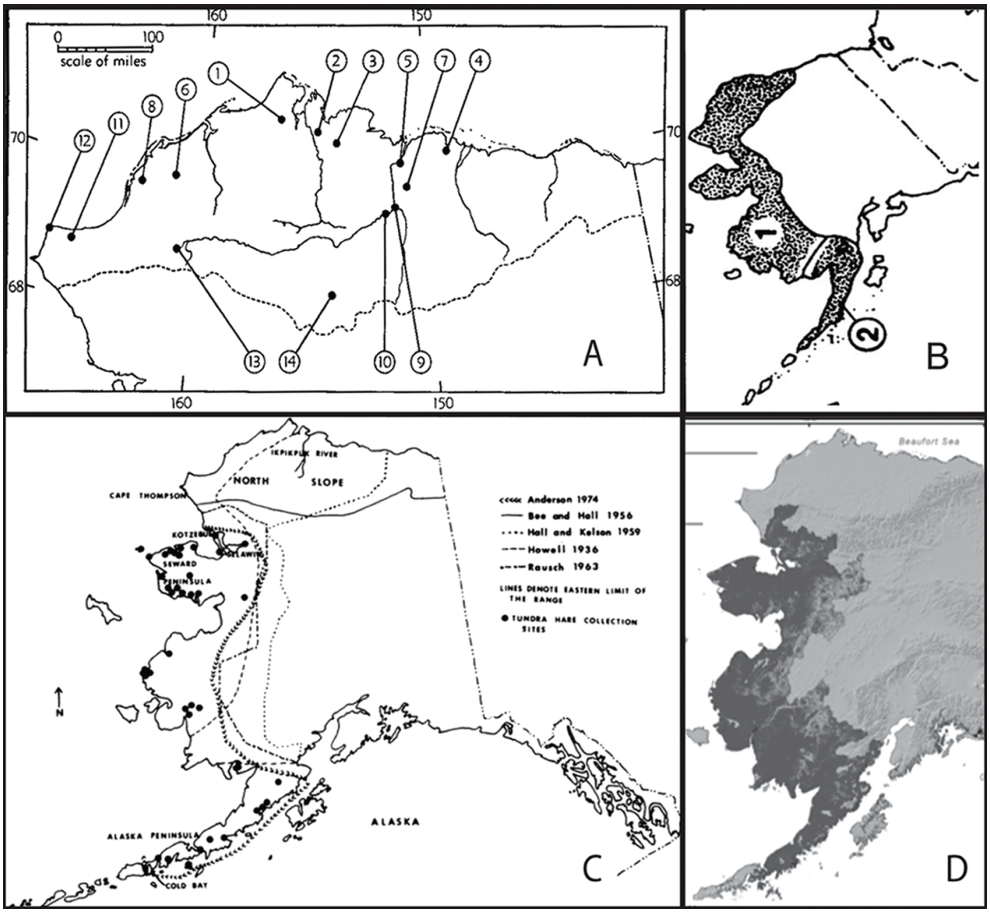
The Alaska Hare (*Lepus othus* Merriam 1900) is the largest hare in North America (Feldhammer et al. 2003) and is the only terrestrial vertebrate with a distribution restricted to the vast roadless, unforested region of western Alaska south of the Brooks Range (MacDonald and Cook 2009). Despite these distinctions, little is known about its natural history, ecology, population dynamics, or distribution. Far more research has been conducted on the two other species in the northern hare complex, the Arctic Hare (*Lepus arcticus* Ross 1819) from northern Canada and the Mountain Hare (*Lepus timidus* Linnaeus 1758) from northern Eurasia, each of which occupies a much larger current range than does *L. othus*. For the purpose of disambiguation, we follow MacDonald and Cook (2009) in referring to *L. othus* as the "Alaska" and not "Alaskan" Hare, since there are two hare species native to Alaska and therefore two "Alaskan hares." Similarly, we capitalize formal common names.

The unique distribution of *L. othus* has been the source of confusion for over a century (Fig. 1). Until now, there has been no verifiable evidence of the occurrence of *L. othus* on the tundra north of the Brooks Range (the North Slope hereafter), but historical anecdotal accounts dating from the late 19th through the mid-20th century (Bee and Hall 1956) continue to influence published range maps (e.g., Klein 1995; Wilson and Ruff 1999; Feldhammer et al. 2003) (Fig. 1). The only specimen purportedly collected from the North Slope was acquired by the 1898 Arctic expedition led by Edward Avery McIlhenny, who obtained a large hare from near Point Barrow (Stone 1900). The fate of this specimen has long been unknown and subsequent researchers have been unable to confirm its identification (Anderson 1978) and have even reported it lost (Bee and Hall 1956). As a result, no North Slope records or specimens were included in MacDonald and Cook's (2009) distribution map of *L. othus*. Reported measurements (Stone 1900) indicated that the skeleton was too large to be Snowshoe Hare (*Lepus americanus* Erxleben 1777), leading Anderson (1978) to provisionally identify the specimen sight unseen as *L. othus*. Out of 318 *L. othus* specimens available for study, it remains the only purported voucher from anywhere north of the Brooks Range.

The most comprehensive study of the natural history and systematics of *L. othus* (Anderson 1974) included a map of all known collection localities of the 189 then-known specimens. The range map encompassed the west coast of Alaska, from the southern Alaska Peninsula to the Kotzebue Sound region, but did not include the North Slope (Anderson 1978). By 1974, there had been no additional sightings of *L. othus* on the North Slope, "despite increased biological investigations associated with recent oil and gas activities" (Anderson 1978, p. 73). Industrial development on the North Slope has increased since the 1970s, along with the biological research required to assess environmental impacts. To date, there have been no sightings reported from the North Slope since 1950 and no large-bodied hare specimens collected since 1898.

Because no voucher specimens could be located, the historical occurrence of *L. othus* north of the Brooks Range has been uncertain. Forest cover is expected to increase and low shrub habitat is expected to decrease in northwest Alaska over the next century (Jorgenson et al. 2015). *Lepus othus* is projected to lose 5% of its habitat in the national public lands of the region (Bering Land Bridge National Preserve, Cape Krusenstern National Monument, Gates of the Arctic National Park and Preserve, Kobuk Valley National Park, Noatak National Preserve, and Selawik National Wildlife Refuge) by the year 2100 (Marcot et al. 2015). However, other

Fig. 1. Previously published distribution maps for *Lepus othus*. (A) North Slope distribution of *L. othus* from Bee and Hall (1956). All localities except number 2 (the locality estimate for the McIlhenny specimen) are based on second- or third-hand anecdotal accounts made to the authors. (B) Distribution from Best and Henry (1994), reproducing the distribution from Hall (1981). (C) Distribution from Anderson (1978) with specimen collection localities and distributions mapped by Howell (1936), Bee and Hall (1956), Hall and Kelson (1959), Rausch (1963), and Anderson (1974). (D) Distribution from Alaska Gap Analysis Project (http://aknhp.uaa.alaska.edu/zoology/akgap/).

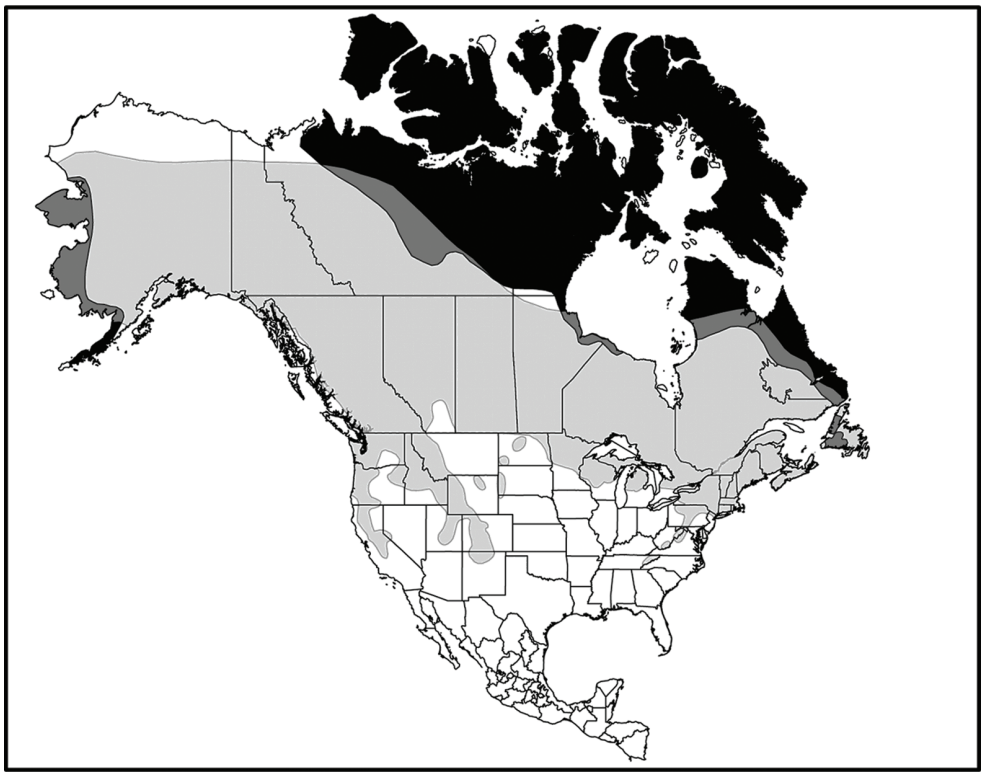


species distribution models (Leach et al. 2015) predict an 80% increase in the bioclimatic envelope of *L. othus* between the beginning of the 20th and end of the 21st centuries, along with a 3% mean latitudinal increase.

Lepus othus feeds on willow (*Salix* spp.), crowberry (*Empetrum nigrum*), and various other ericaceous plants, grasses, sedges, and lichens (Anderson 1974). It is preyed on by both Red Fox (*Vulpes vulpes*) and Arctic Fox (*V. lagopus*), and Golden Eagles (*Aquila chrysaetos*) (Anderson 1974). *Lepus othus* remains (University of Alaska Museum (UAM) Mammal Collection specimen 113979) have also been found in Gyrfalcon (*Falco rusticolus*) nests. Other likely predators include Snowy Owl (*Bubo scandiacus*), Gray Wolf (*Canis lupus*), and Rough-legged Hawk (*Buteo lagopus*) (Anderson 1974).

Potential ecological interactions between *L. othus* and the only other native leporid in Alaska, the Snowshoe Hare (*L. americanus*), has been suggested but not directly studied (Klein 1995). The two species are sympatric throughout much of western Alaska (MacDonald

Fig. 2. IUCN range maps (Murray and Smith 2008a,b,c) of *Lepus othus* (black, western Alaska), *Lepus arcticus* (black, northern Canada), and *Lepus americanus* (light gray). Range overlap is shown in dark gray. The range of *L. arcticus* extends north and northeast off panel.



and Cook 2009) (Fig. 2) and are frequently confused due to their similar pelage. *Lepus americanus* occurs throughout most of mainland Alaska except the western half of the Seward Peninsula and all but the easternmost terminus of the Alaska Peninsula (ADFG; MacDonald and Cook 2009) while *L. othus* is restricted to coastal western Alaskan (MacDonald and Cook 2009).

In light of the inordinately rapid pace of environmental change in Alaska's Arctic and coastal tundra regions, the unique and restricted yet poorly understood range of *L. othus*, and the four decades that have elapsed since the distribution of this Alaskan endemic was last rigorously evaluated, we conducted an extensive review of the present distribution of *L. othus*. We hypothesized that there is no evidence to include the North Slope in the present distribution of *L. othus* and that the historical anecdotal accounts from the North Slope could not be corroborated by voucher specimens. Our review was based on museum specimens, photographs, literature records, and credible observations. We also compared the known distribution based on these data to a spatial distribution model for *L. othus*.

Materials and methods

We surveyed 39 North American and Canadian museums (Appendix Table 1) for *L. othus* specimens through online database searches, contact with curators and collection managers, and (or) personal visits. All known *L. othus* specimens are listed in Supplementary Material Table 1[1]. Museums surveyed but not listed in Table S1 had no *L. othus* specimens.

[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2015-0019.

We confirmed identifications by skull size and (or) winter pelage coloration (see below) through personal inspection or photographs from curators and collection managers. Where neither was possible, we considered the familiarity of the collector or identifier with both *L. othus* and the only other hare known to occur in sympatry and with which it is occasionally confused, *L. americanus*. *Lepus othus* in its winter pelage is easily identified by distinctive black-tipped ears and fur that is white to the roots. Winter pelage of *L. americanus* is white tipped with dark roots and does not include black fur on the inner tips of the pinnae (although black may be present along the edges).

In addition to traditional voucher specimens, we included accounts of *L. othus* catalogued and curated as observations in the Mammal Collection of the UAM. We evaluated these records on a case-by-case basis prior to cataloguing, and they generally included photographs or video to corroborate identification. In some cases, observer expertise alone was considered sufficient following interviews by museum staff. Catalog numbers for UAM observations are denoted with the prefix "UAMObs."

Lepus othus specimens with collection locality descriptions but without geographic coordinates were assigned coordinates (WGS 84 datum) and error radii with the georeferencing platform GEOLocate (Rios and Bart 2014). Misspelled place names were corrected according to the Dictionary of Alaska Place Names (Orth 1971). Locality descriptions that were not recognized by GEOLocate were manually assigned coordinates and error radii with Google Earth Pro v. 7.0.3.8542. Error radii were determined according to BioGeoMancer standards for estimating error from locality descriptions (Chapman and Wieczorek 2006). Locations with error radii exceeding 200 km were georeferenced but not included in Fig. 3. Place names or descriptions that could not be located were not assigned coordinates and are not shown in Fig. 3 but are included in Table S1. We georeferenced all specimens collected between 1877 (the earliest known modern *L. othus* specimen) and 2014. We did not examine paleontological or zooarchaeological material, which tends to be fragmentary and identified in the literature and (or) on collections databases to genus level only.

We used RandomForests (Salford Systems, Inc., San Diego, California; www.salford-systems.com) to create a spatial distribution model for *L. othus*. The resulting model accounts for the confounding and nonlinear relationships among variables (Breiman 1996; Cutler et al. 2007). Collection localities (Table S1) with accuracy within 100 km were used as presence points for the spatial distribution model. Presence locations and 500 randomly distributed pseudo-absence points for *L. othus* were attributed with 28 environmental predictor layers (Table 1) using the extract values to multipoint tool in ArcGIS 10.3.1 (ESRI, Inc., Redlands, California) and used as training data to develop the model in RandomForests. The model was grown to 1000 trees, considered eight predictors at each node, and used all other software default settings. Aspatial performance was cross-validated internally in RandomForest using an "out-of-bag" set of training points (Breiman 1996). The discrimination capacity of each model was assessed using resultant sensitivity and specificity of the out-of-the bag data set and the area under the curve (AUC) based on the receiver-operating characteristic (ROC). The model was applied in ArcGIS 10.3.1 to a grid of points distributed at 1 km intervals across Alaska that were also attributed with the same environmental predictors. Model outputs generated relative indices of occurrence (RIO) for each point, which is a ranking of pixels from 0 to 1 representing the likelihood of belonging to the "presence" class. A balanced threshold of 0.55 was used to differentiate between presences and absences for all models. For continuous visualization between points, predicted RIO values were rasterized using the Inverse Distance Weighting (IDW) tool using a 1-km resolution and clipped to the state coastline. RandomForests was also used to rank the relative importance of the environmental variables in the model.

Fig. 3. Collection localities of all catalogued *Lepus othus* museum specimens and observations, other localities discussed in text, and the distribution boundary from Anderson (1974).

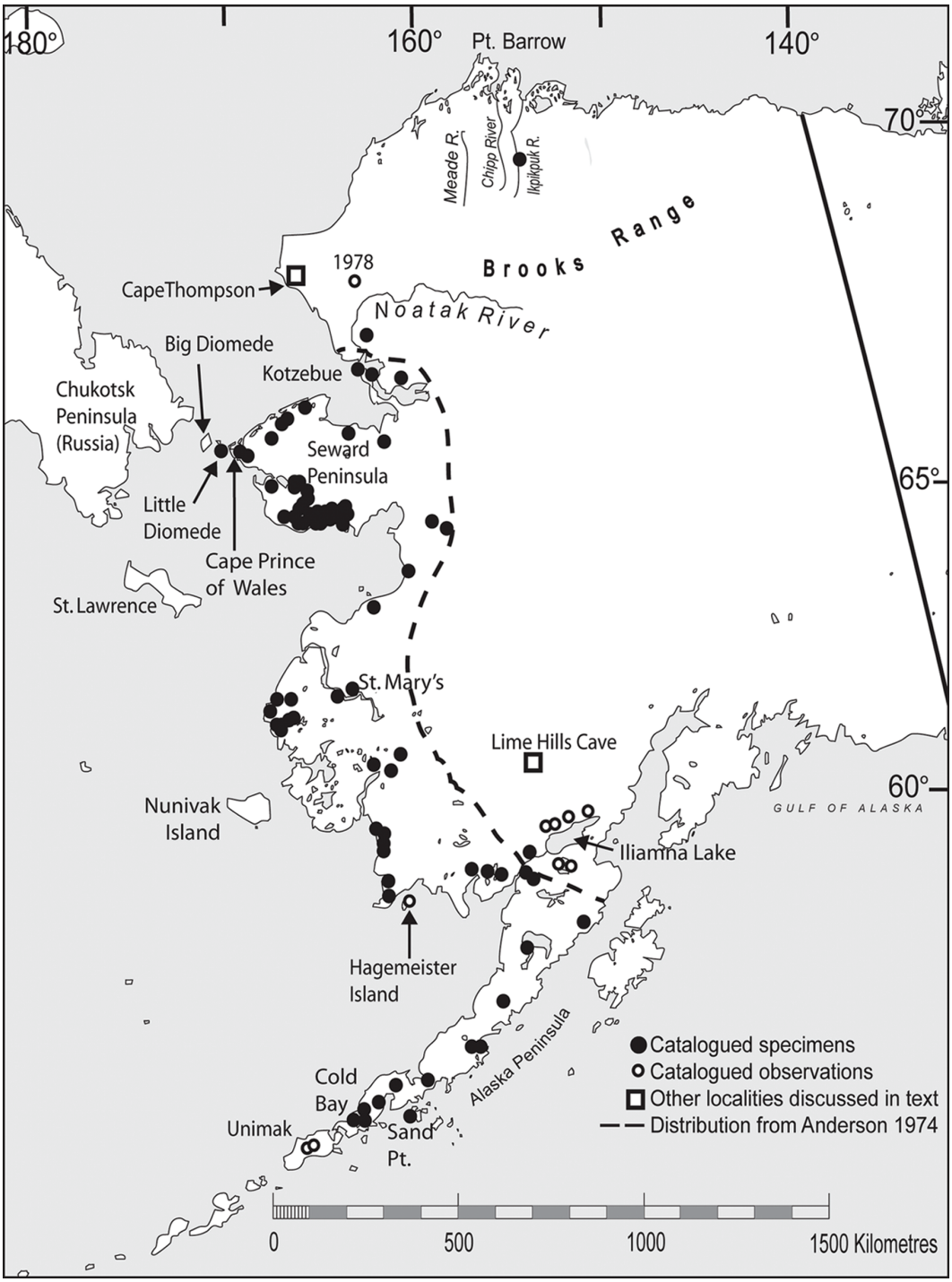


Table 1. Environmental variables and their relative importance to the spatial distribution model.

Variable	Relative score
Distance to March sea ice	100.00
Distance to coastline	68.22
Cliome	47.74
Geology	36.26
Elevation	28.30
Mean temperature for September/October/November	21.91
Mean % of days where precipitation fell as snow in September/October/November	10.21
Mean first day of freeze	8.36
Mean % of days where precipitation fell as snow in March/April/May	7.27
Mean temperature for March/April/May	5.47
Mean % of days where precipitation fell as snow in December/January/February	5.42
Mean ground temperature	5.03
Mean temperature for December/January/February	4.49
Distance to September sea ice	3.85
Mean first day of thaw	3.84
Distance to lakes	2.51
Mean number of grow days	2.02
Mean temperature for June/July/August	1.98
Mean % of days where precipitation fell as snow in June/July/August	1.57
Mean precipitation for September/October/November	1.22
Mean precipitation for March/April/May	1.11
Mean precipitation for June/July/August	0.96
Mean precipitation for December/January/February	0.76
Mean active layer thickness	0.74
Distance to streams	0.63
Aspect	0.45
Distance to wetland vegetation	0.41
Slope	0.23

Results

We located 318 specimens of *L. othus* from 12 museum and other collections and were able to georeference 305 from their locality descriptions (Fig. 3; Table S1). Many were already associated with geographic coordinates available from the host museum. These localities spanned much of Alaska's west coast but the majority (175) of specimens were collected from the Seward Peninsula (Fig. 3). The current northernmost range limit was extended approximately 50 km north after collection of the first *L. othus* voucher (UAM 120460) from Noatak National Preserve in April 2014. There was also a credible sighting (UAMObs 213) of an *L. othus* individual in 1978 in the western Brooks Range approximately 150 km northeast of where UAM 120460 was collected. The southernmost specimens were collected in Cold Bay, approximately 50 km from the terminus of the Alaska Peninsula, as recently as 1993 (UAM 42143). We personally confirmed the species identification of the northern- and southernmost specimens, both of which are housed at UAM. Most specimens were collected close to Alaska's western coastline. The inland-most specimens were collected near St. Mary's, less than 150 km from the coast. Several reliable observations (UAMObs 219-225) originated near Iliamna Lake, which is farther east than almost all specimen collection localities but less than 100 km inland from the Gulf of Alaska.

We located the "lost" McIlhenny specimen (CMN 31930), a skull and postcranial skeleton collected from near Barrow, in the Mammal Collection at the Canadian Museum of Nature. Data on the specimen tag confirm that it is the same specimen listed in the expedition's report (Stone 1900). We borrowed the specimen and verified that the craniodental measurements were within the range of the *L. othus* specimens measured by Anderson (1974) and exceeded the maximum basilar skull length of *L. americanus* (67 mm) reported by Hall (1981). Visual comparisons also confirmed that it is not *L. americanus*.

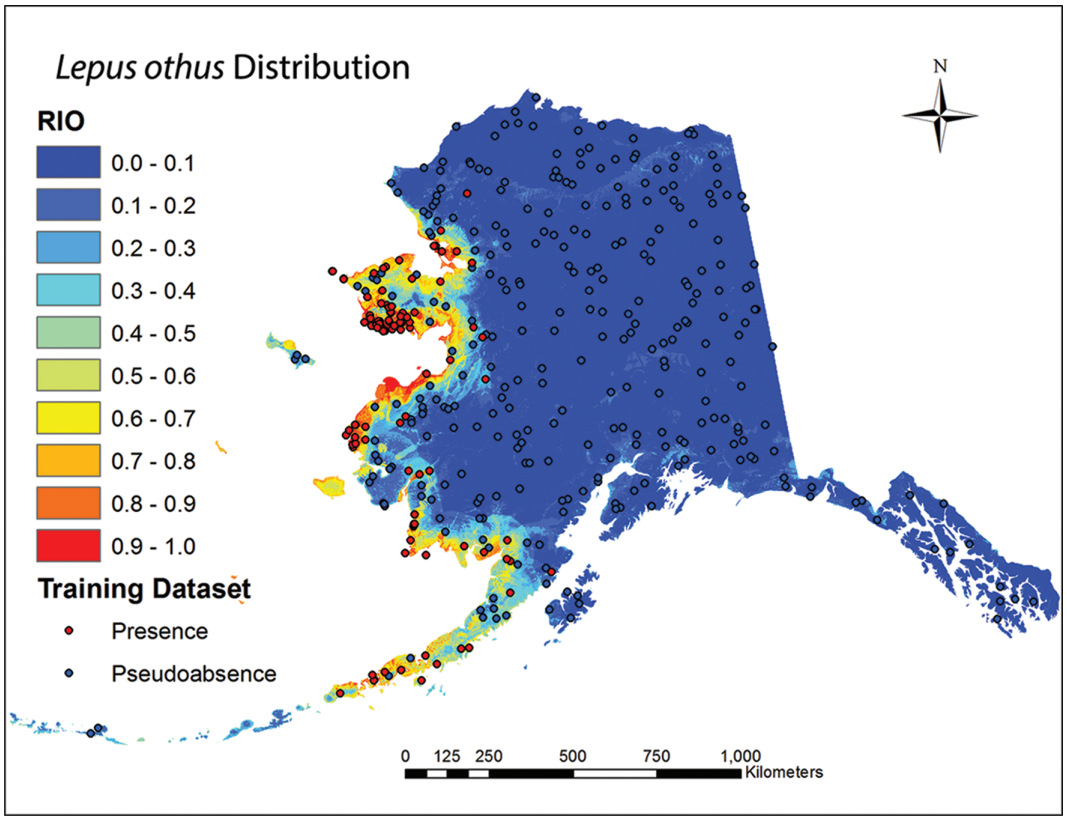
Two new credible observations of *L. othus* on Unimak Island (the easternmost of the Aleutian Islands) in 2013 and 2014 (UAMObs 182, UAMObs 192) were reported, and a photograph of an *L. othus* individual on Hagemeister Island (UAMObs 181) was taken by a camera trap at a walrus haulout site in 2013. Both Hagemeister and Unimak are close to mainland Alaska (<5 and <1 km, respectively) and are sometimes connected to the mainland by sea ice in late winter and early spring. Additionally, one or more very large hares fitting the description of either *L. timidus* or *L. othus* were reported from St. Lawrence Island (Fig. 3) in the winter of 2012 (G. Sheffield, personal communication) and are the first known sighting of a hare on that island. Prior to this study, Alaska Hares were not known from any of these islands.

Russia's Chukotsk Peninsula and Alaska's Seward Peninsula are 80 km apart. Midway between them lie the two Diomede Islands. Large-bodied hares currently identified as *L. othus* have been collected from Little Diomede Island in 1936 (USNM 260900) and more recently in 2014 (UAM 120797, UAM 122839) but have only been sporadically reported from the island. During winter 2013–2014, several hares were observed on Little Diomede (including the two UAM specimens). UAM 120797 was pregnant with seven near-term embryos when shot by subsistence hunters in June 2014. Little Diomede lies 37 km west of Alaska's Seward Peninsula and less than 4 km east of Russia's Big Diomede Island, which in turn is only 35 km east of the Chukotsk Peninsula; all are interconnected by sea ice for up to 6 months out of the year (NSIDC 2013). In the 1960s, bush plane pilot Bill Munz reportedly saw a "huge" aggregation of large-bodied hares moving east on the sea ice between Little Diomede Island and Cape Prince of Wales (J. Jacobson, personal communication) (Fig. 3), which is on the western tip of the Seward Peninsula. Whether the hares collected from Little Diomede in 2014 represent *L. othus* from Alaska or *L. timidus* from Russia remains unclear, as does the present occurrence of hares on Big Diomede. However, residents on Little Diomede recounted the regular occurrence of hares on Big Diomede and sporadic dispersal to Little Diomede (personal communication to J.J.B.) in the 1960s.

Curiously, no specimens or observations of hares are known from Nunivak Island (Fig. 3), the second-largest island in the Bering Sea and only 30 km from mainland western Alaska, to which it is seasonally connected by sea ice. Residents and hunting guides on Nunivak report that hares do not occur on the island (W. Don, personal communication). Our spatial distribution model (Fig. 4) predicts their likely presence on Nunivak, but the reason(s) for the apparent absence of *L. othus* there remains unknown.

Murie (1959) noted the absence of *L. othus* on Unimak Island (Fig. 3) after his faunal survey of the Alaska Peninsula and Aleutian Islands in the 1930s. MacDonald and Cook (2009) reported no island records from southwest Alaska, aside from a failed introduction on Chirikof Island (Fig. 3). However, one specimen (USNM 203278; identification confirmed by L.E.O.) is listed as having been collected from Sand Point (Fig. 3), on Popov Island, in 1913. Popov Island is not surrounded by sea ice in the winter, and ocean currents in the Unga Strait separating the island from the southern coast of the Alaska Peninsula are strong and constant. The village of Sand Point was, like Barrow, a trading center for many years; it is possible that the specimen may have been collected on the mainland and brought to Sand Point. Alaska Hares are not known to occur on Popov Island today, and Snowshoe Hares introduced to the island in 1955 are reported to be abundant (MacDonald and Cook 2009;

Fig. 4. Spatial distribution model of the present distribution of *Lepus othus*. Red circles mark presences (georeferenced collection localities). Blue circles indicate pseudoabsences. Relative indices of occurrence (RIO) values greater than 0.55 indicate regions of likely presence, and values less than 0.55 indicate regions of likely absence.



D. Watts, personal communication). The two observations of *L. othus* on Unimak (UAMObs 182 and UAMObs 192) and a photograph of *L. othus* on Hagemeister (UAMObs 181) are additional evidence of *L. othus* on islands in southwestern Alaska.

The spatial distribution model closely matched the known distribution based on specimen and observation localities (Fig. 4). The ROC value was 0.98, the balanced error rate was 0.06, the sensitivity was 94.24%, and the specificity was 94.00%. Distance to March sea ice and the distance to the coastline were the most important variables in the model (Table 1). The northernmost specimen collection locality is in an area of likely *L. othus* presence, as predicted by the spatial distribution model. However, the location of the northernmost credible observation is in the midst of the Brooks Range, where the model predicts the absence of *L. othus*. The model did predict the presence of *L. othus* on St. Lawrence Island, despite the pseudo-absence localities used in the data set. We did not include the observation of a large-bodied hare on St. Lawrence Island as a presence point because we received it third-hand and it is not considered a catalogued observation.

Discussion

Based on the collection locality of UAM 120460, we consider the current northernmost known range limit of *L. othus* to be approximately 50 km northeast of Kotzebue. Prior to the acquisition of this specimen and the "rediscovery" of CMN 31930 from the North Slope,

the northernmost *L. othus* voucher was collected in the Kotzebue area (UAM 4132). In May 1978, a *L. othus* individual was sighted 190 km northeast of Kotzebue, well into the Brooks Range (UAMObs 213), by a professional hunting guide very familiar with both *L. othus* and *L. americanus*. The spatial distribution model expects the northernmost range extent of *L. othus* to be near Kivalina, which is about 105 km northwest of the northernmost collection locality. We consider the range of *L. othus* to include the area in which the species is consistently found while acknowledging what are likely dynamic boundaries, particularly along the northern limit of its core range. Therefore, we do not consider the current distribution of *L. othus* to include the North Slope. The absence of *L. othus* on the vast tundra landscape of Alaska's North Slope remains vexingly inexplicable and warrants thorough exploration.

The McIlhenny expedition reported the "Ikpikpun river" as the collection location of the North Slope specimen (Stone 1900, p. 30). However, the donor of the specimen, Charles Brower, reported having the hare brought to him in 1897 from "inland on the Chipp River" and later giving "the whole animal to E. A. McIlhenny, who sent it out with his collection" (Howell 1936, p. 334). Although we could not locate an "Ikpikpun River" on contemporary maps of Alaska, the Ikpikpuk River is about 50 km east of the Chipp River and lies approximately 100 km southeast of Point Barrow. The Smithsonian Contributions to Anthropology described the location of the Ikpikpun River as east of Point Barrow (Stanford 1976) and Murdoch (1892) described it as about 40 miles east of the Meade River, which is the approximate location of the Ikpikpuk River. We therefore conclude that the specimens reported by both Brower and the expedition (stationed in Point Barrow between August 1897–1898) are one and the same.

Long-distance dispersal (200 km) has been documented in *L. timidus* (Angerbjörn and Flux 1995) and it is likely that *L. othus* has occasionally dispersed well outside the species' current core range. According to both the expedition report (Stone 1900) and Brower (Howell 1936, p. 334), CMN 31930 was collected on the North Slope and not transported there by hunters or traders (although not an Alaska Native, Brower spoke fluent Iñupiaq). It is possible that Brower's understanding of the collection locality was incorrect and the hare was killed elsewhere and brought to the North Slope, perhaps via a series of trades. However, the fact that external measurements were recorded (Stone 1900) indicates that the specimen was an intact carcass available to either the expedition or Brower. An entire *L. othus* brought to the Point Barrow region from the closest point of its current distribution (about 500 km away) seems cumbersome but possible, especially with winter sled dog travel when the hare could be kept frozen and long-distance travel was common (Burch 1988). If, however, it was collected at its reported location, it may represent an anomalous disperser from northwest Alaska that made its way to the North Slope along the coast.

In their seminal but contentious book, Bee and Hall (1956) included the North Slope in the range of *L. othus* (Fig. 1). However, they did not examine any specimens to vouch for a North Slope occurrence, and others (Buckley and Scott 1957) criticized the authors' limited field research and dependence on personal communication. The McIlhenny specimen from near Point Barrow (which Bee and Hall proclaimed lost or misplaced) was the only evidence to corroborate any of Bee and Hall's North Slope records; the other 13 localities represented second- or third-hand accounts. Our exhaustive search did not locate any specimens to confirm Bee and Hall's other locality records. The McIlhenny specimen provides the only verifiable evidence that at least one Alaska Hare occurred on Alaska's North Slope in the late 19th century.

Questionable field identifications may have contributed to anecdotal reports of *L. othus* on the North Slope. John Murdoch, an early naturalist and source for Bee and Hall (1956), reported that Alaska Natives in Point Barrow were unfamiliar with *L. othus* but that the "Nunatangmeau" Eskimos brought hare skins there for trade. He considered these skins

evidence of "polar hares" occurring "somewhere in the Colville Region" (Murdoch 1885:103). However, the dark roots of the fur on these skins, which are catalogued (USNM E89915-0 and USNM E89915-1) in the Anthropology Collection of the United States National Museum of Natural History, confirm that they are *L. americanus*. It is likely that the authors of many early reports may not have been able to differentiate between *L. othus* and *L. americanus* or between traveling Alaska Native groups, which casts further doubt on the validity of these records.

Another possible *L. othus* specimen from the North Slope resides at the California Academy of Sciences (CAS 23818). The specimen is a discolored pelt without head or feet but with pelage resembling that of *L. othus*. According to the limited associated data, it was purchased from a trader in Barrow, Alaska, in the early 1960s. The skin tag identifies the specimen as an "Arctic Hare *Lepus arcticus*," a close relative of *L. othus* that ranges across much of northern Canada but does not occur in Alaska. However, the term "Arctic hare" to this day is commonly, if erroneously, used to refer to *L. othus*. If the animal was collected in the Barrow area, it was likely *L. othus*. The hide was tanned, a process that significantly damages DNA, and we cannot conclusively identify the specimen as *L. americanus*, *L. othus*, or *L. arcticus* on visual inspection. In light of the uncertain provenance and identification, we do not consider it to be a credible voucher.

Zooarchaeological evidence of *L. othus* has been reported from Cape Thompson (Fig 3) (Pruitt 1966), where bones and teeth identified as *L. othus* were discovered in the remains of 150- to 200-year-old Eskimo dwellings. However, it is unclear if *L. othus* actually occurred at Cape Thompson or was hunted elsewhere and brought there. Other archaeological and zooarchaeological remains from Alaska include numerous specimens identified as "*Lepus* sp." or as "*Lepus othus* or *Lepus americanus*" (AMNH:FAM:99926; Yesner 2001). Identification of these remains would provide valuable insight into the past distribution of both species.

No other extant mammal is restricted to coastal western and southwestern Alaska without also being found on the North Slope (MacDonald and Cook 2009), and it is unclear why the current distribution of *L. othus* is apparently limited to south of the Brooks Range. The closely related and morphologically indistinguishable *L. arcticus* is found much farther north in Canada (Fig. 2) in more extreme environments than are found on Alaska's North Slope. The presumed expansion of *L. americanus* to the North Slope indicates that the mountains of the Brooks Range are not a significant barrier to hares. The 1978 sighting of *L. othus* well within the western Brooks Range (UAMObs 213) may indicate the occurrence of occasional long-distance dispersers north of the current range extent or stepwise dispersal over multiple generations. Although there is no apparent biogeographic barrier, the western distribution of *L. arcticus* likewise appears to end abruptly in the Northwest Territories, Canada, and does not extend to Alaska's North Slope. Waltari et al. (2004) concluded that the Mackenzie River, in northwest Canada, is a boundary between the two species, which may have expanded from two different glacial refugia, as has been hypothesized for small mammals such as the Collared Lemming, *Dicrostonyx groenlandicus* (Fedorov and Stenseth 2002). Porsild (1945) reported unspecified evidence that he attributed to *L. arcticus* in the Richardson Mountains west of the MacKenzie River in July 1933 and on gravel ridges in the foothills between the Mackenzie Delta and the Alaska border. However, it remains unclear why northern hares, medium-sized mammals that have been recorded dispersing over great distances (Angerbjörn and Flux 1995), do not occur on the tundra north of the Brooks Range. The spatial distribution model does not predict the presence of *L. othus* on the North Slope, which may be unfavorable to northern hares for as-yet unknown reasons, such as snow pack and terrain.

It is unclear if the apparent northward expansion of *L. americanus* has affected the geographic range of *L. othus*. There is little mention of *L. americanus* north of the Brooks Range

before the 1990s (Klein 1995; MacDonald and Cook 2009) except along waterways with willows "at times of high population" (Manville and Young 1965, p. 16). Tape et al. (2015) calculated that shrub height in northern Alaska reached the threshold required by *L. americanus* between 1964 and 1989.

Unlike *L. arcticus* and *L. othus*, *L. timidus* is found in boreal forest in addition to alpine and tundra habitat, possibly because *L. americanus*, which thrives in the boreal forests of North America, does not occur in Eurasia. *Lepus arcticus* can survive at low densities in shrub or partially forested habitat in the absence of mammalian predators and competition from *L. americanus* (Small and Keith 1992). *Lepus othus* may be able to similarly persist in forested habitat. In Newfoundland, *L. americanus* has been shown to be more resilient than *L. arcticus* to predation by Red Foxes (Small and Keith 1992), possibly by favoring understory cover. *Lepus arcticus* may also struggle to escape predators in the soft, deep snow in Newfoundland's shrub and forest habitat where *L. americanus* is more successful (Mercer et al. 1981). The more abundant prey species, *L. americanus*, may have caused a "high density of randomly foraging [shared] predators that 'spill over' into other habitats and decrease the abundance and distribution of alternative prey," in this case, *L. arcticus* (Small and Keith 1992, p. 1620). Red Foxes have expanded their range in Alaska and other northern regions (Killengreen et al. 2007; Post et al. 2009), moving north of the Brooks Range in the 20th century but largely keeping to the foothills and river corridors except during occasional periods of abundance on the tundra plain of the North Slope (Savory et al. 2014). Red Foxes did become more common on the North Slope in the late 20th century, especially in association with oil development infrastructure, but *L. othus* persists in western Alaska in partial sympatry with *L. americanus* and *V. vulpes*, so the evidence does not support predator spillover as the cause for the potential disappearance of *L. othus* from north of the Brooks Range.

Zooarchaeological evidence suggests that *L. americanus* has replaced *L. othus* in the Lime Hills Cave region (Fig 3), located in what was formerly tundra/alpine habitat but is now boreal spruce–birch forest (Endacott 2008). Endacott (2008) identified all hare remains from the deepest soil strata (late Wisconsin, 14 000 years ago) as *L. othus* and all hare remains from the top strata (≥8000 years ago) as *L. americanus*. The middle strata (14 000–8000 years ago) contained remains of both species. This pattern has been interpreted as being "clearly the result of reduced tundra/alpine habitat in the area and expansion of shrubs and boreal forest" (Endacott 2008, p. 233), a shift in habitat similar to the present expansion of shrubs and trees into former Arctic tundra (Hinzman et al. 2005), although on vastly different time scales. Archaeological remains identified as *L. othus* have been reported from interior Alaska (Weber et al. 1981; Dixon 1984), which is now predominantly boreal forest and well outside the current distribution of *L. othus*. Zooarchaeological and ethnological material could provide a better understanding of the historical distribution of *L. othus* and how it has changed over time. However, a combination of ancient DNA extracted from Beringian paleontological hare remains, together with orders of magnitude more molecular markers than have been employed in the past, will almost certainly be required for definitive resolution.

Taxonomy and gene flow

Consideration of the Alaska Hare's distribution requires an understanding of its tortuous taxonomic history and current status. *Lepus othus* is part of a species complex comprising the subgenus *Lepus* Linnaeus 1758, which currently includes two other northern hare species: the Arctic Hare (*L. arcticus*) and the Mountain Hare (*L. timidus*). As currently circumscribed taxonomically, *L. othus* is restricted to western Alaska, *L. arcticus* occurs in Greenland and northern Canada from the Northwest Territories to Newfoundland and Ellesmere Island, and *L. timidus* ranges from the Chukotsk Peninsula in far eastern Russia to eastern

Poland, throughout Scandinavia, and in isolated populations in Japan, the British Isles, and the Alps (Angerbjörn and Flux 1995).

Geography and allopatry are the principal grounds upon which *L. othus*, *L. arcticus*, and *L. timidus* have retained their separate species status (Anderson 1974). Morphological (Baker et al. 1983; Dixon et al. 1983) and molecular (Waltari and Cook 2005; Alves et al. 2008; Melo-Ferreira et al. 2012) data have been inconclusive or conflicting, and the taxonomy of northern hares remains in dispute. Ranges of the three species are not thought to overlap and therefore gene flow is not thought to occur (Anderson 1974).

The identification (*L. othus* or *L. timidus*) of the northern hare sighted on St. Lawrence Island in winter 2012 is unclear. St. Lawrence is 75 km from the Chukotsk Peninsula but 190 km from the nearest Alaskan mainland, suggesting that the hare(s) in question likely originated from Russia. Thus, presumably infrequent but recurrent gene flow between the two species may be facilitated by island stepping stones, especially if their thick pelage is providing sufficient insulation to forgo foraging for up to 15 days, as has been theorized for *L. arcticus* (Wang et al. 1973). Wolverine (*Gulo gulo*) and Brown Bear (*Ursus arctos*) are also observed on St. Lawrence Island occasionally, although there are no sustaining populations of either species on the island (as communicated by residents to J.J.B.). However, as climate change continues to affect sea ice extent in the Arctic (Bernstein et al. 2007), there could be a reduction in potential gene flow between in Eurasia, Alaska, and the islands between the two continents.

Clarifying the distributional limits of *L. othus* will require resolution of northern hare taxonomy given the potential for gene flow between *L. timidus* from eastern Russia and *L. othus*. When the McIlhenny specimen was collected, it was originally identified as *Lepus tschuktschorum* Nordquist 1883 (Stone 1900), a junior synonym of *L. othus* that included northern hares from Eastern Siberia and Alaska. If eastern Siberian hare populations are considered conspecific with *L. othus*, then "[*Lepus*] *tschuktschorum* Nordquist, 1883 has priority over [*Lepus*] *othus* Merriam, 1900" (Hoffmann and Smith 2005, p. 202).

It is widely agreed that high-latitude regions have been impacted by climate change in the past century and are likely to be inordinately affected by continuing changes in phenology, vegetation cover, snow cover, and ground icing conditions (Hinzman et al. 2005; Bernstein et al. 2007; Prowse et al. 2009; Jorgenson et al. 2015). These changes could make foraging more difficult for herbivores. Shrub cover in the Alaskan Arctic has increased over the past century and is expected to continue to expand, and treeline encroachment into formerly tree-less areas has been documented in western and northern Alaska (Hinzman et al. 2005; Prowse et al. 2009). Such conditions will likely favor the continued expansion of *L. americanus* into northern and western Alaska. Tundra-associated mammals such as the Barren Ground Shrew (*Sorex ugyunak*) and Singing Vole (*Microtus miurus*) are predicted to undergo range shifts away from western and southern extents of Arctic tundra (Hope et al. 2013; Baltensperger and Huettmann 2015).

Although the historical occurrence and abundance of *L. othus* on the North Slope remains unclear, a northern shift from its current range is predicted by Leach et al. (2015) and may be critical to its long-term viability. Most of the western North Slope lies within the National Petroleum Reserve – Alaska (NPR-A), federal land set aside for potential oil and gas operations. The US Bureau of Land Management has noted the current presumed absence of *L. othus* in its environmental impact statement for the NPR-A (BLM 2012). However, by the end of the 21st century, this region may be the only large expanse of continuous unforested habitat left in Alaska (Prowse et al. 2009; Hope et al. 2013) and much of the shifted range of *L. othus* as predicted by Leach et al. (2015) lies within the NPR-A, a prospect that echoes recent calls (reviewed by Hannah 2011) for considering probable future range shifts in conservation and management plans.

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Appendix

Table A1. Names and abbreviations of museums and other collections searched through online databases, contact with curators and collection managers, and (or) personal visits.

Museum name	Museum abbreviation
Academy of Natural Sciences	ANSP
American Museum of Natural History	AMNH
Burke Museum of Natural History and Culture, University of Washington	UWBM
California Academy of Sciences	CAS
Canadian Museum of Nature	CMN
Carnegie Museum	CM
Charles R. Connor Museum	CRCM
Cornell University Museum of Vertebrates	CUMV
Cowan Vertebrate Museum, University of British Columbia	UBC
Denver Museum of Nature and Science	DMNS
Dickey Collection, University of California, Los Angeles	UCLA
Field Museum of Natural History	FMNH
Humboldt State University Wildlife Collection	HSUW
Izembek NWR	
James R. Slater Museum of Natural History, University of Puget Sound	PSM
Los Angeles County Museum	LACM
Louisiana State University, Museum of Natural Science	LSUMZ
Michigan State University Museum	MSU
Monte L. Bean Life Science Museum, Brigham Young University	BYU
Museum of Comparative Zoology, Harvard	MCZ
Museum of Southwestern Biology, University of New Mexico	MSB
Museum of Texas Tech University	TTU
Museum of Vertebrate Zoology, University of California	MVZ
New Mexico Museum of Natural History	NMMNH
New York State Museum	NYSM
Oklahoma Museum of Natural History, University of Oklahoma	OMNH
Royal British Columbia Museum	RBCM
Royal Ontario Museum	ROM
Texas Cooperative Wildlife Collection	TCWC
United States National Museum of Natural History (Smithsonian)	USNM
University of Alaska Museum	UAM
University of Alberta Museum of Zoology	UAMAZ
University of California Davis	UCD
University of Colorado Museum	UCM
University of Kansas, Natural History Museum and Biodiversity Center	KU
University of Michigan Museum of Zoology	UMMZ
University of Wisconsin Zoological Museum	UWZM
Utah Museum of Natural History, University of Utah	UMNH
Western New Mexico University	WNMU