Range Contractions of North American Carnivores and Ungulates

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We compared the historic and current geographical ranges of 43 North American carnivores and ungulates to identify large-scale patterns in range contractions and expansions. Seventeen of the species had experienced range contractions over more than 20% of their historic range. In areas of higher human influence, species were more likely to contract and less likely to persist. Species richness had also declined considerably since historic times. The temperate grasslands and temperate broadleaf–mixed forest biomes lost the highest average number of species, while the boreal forest and tundra showed fewer numbers of species lost. Species contractions were a result of Euro-American settlement and postsettlement development in North America. These effects have been widespread and indicate a rapid collapse of species distributions over the course of only 1 to 2 centuries. The results of this study can be used to improve scientists' knowledge of historical reference conditions and to provide input for wildlife reintroductions and for the creation of wildlife reserves.

Keywords: range contractions, wildlife distribution, human influence, historical condition, geographic information systems

Species ranges are dynamic, and knowledge of range contractions and expansions and their underlying causes is important for conservation biology and maintenance of biodiversity. Studies of species range changes have focused on the expansion of introduced species (Andow et al. 1990, Hastings 1996); investigations of species range shapes (Brown and Maurer 1989); the relationship between species distribution and abundance (Gaston 1990); and the relationship between range size, latitude, and elevation (Pagel et al. 1991, Brown et al. 1996). Patterns of range dynamics have also been studied, with some authors concluding that contractions occurred toward the center of the species' historic range (Lawton et al. 1994), while others determined that species ranges contracted toward their edges (Lomolino and Channell 1995, Channell and Lomolino 2000a, 2000b). The latter authors acknowledged that humans were the most likely reasons for range contractions. Although it is well known that humans have altered their environment, until recently few quantitative studies have assessed the degree of human influence, especially on a continental or global scale (Hannah et al. 1994, Dobson et al. 2000, Sanderson et al. 2002). Nor do researchers and land managers have much information about how human influence and species range contractions correlate. This knowledge could be crucial for developing predictions of further range contractions, designing parks and reserves, and managing declining species.

On the basis of the global distribution of 173 mammals, Ceballos and Ehrlich (2002) estimated that collectively those species had lost more than 50% of their historic range. In New Zealand, Towns and Daugherty (1994) found that direct human influences had affected range contractions of reptilians and amphibians, but indirect human effects brought about by the introduction of dogs, cats, and rats were the primary factor for extinctions. In a global study, Kerr and Currie (1995) concluded that human population density strongly influenced the proportion of threatened bird species, but the per capita gross national product showed the strongest correlation with mammal extinctions. In a study conducted in West Africa, Brashares and colleagues (2001) determined that there was a strong positive relationship between human population size and the extinction rate of mammal species. Several studies conducted in the Amazon have shown that human hunting contributed to a lower density of game species and in some

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Table 1. North American carnivores and ungulates included in this study.

Common name	Scientific name
Carnivores	
Black bear	*Ursus americanus*
Grizzly bear	*Ursus arctos*
Polar bear	*Ursus maritimus*
Gray wolf	*Canis lupus*
Coyote	*Canis latrans*
Swift fox	*Vulpes velox*
Kit fox	*Vulpes macrotis*
Arctic fox	*Alopex lagopus*
Red fox	*Vulpes vulpes*
Gray fox	*Urocyon cinereoargenteus*
Cougar	*Puma concolor*
Lynx	*Lynx canadensis*
Bobcat	*Lynx rufus*
Ringtail	*Bassariscus astutus*
Raccoon	*Procyon lotor*
White-nosed coati	*Nasua narica*
River otter	*Lontra canadensis*
American mink	*Mustela vison*
Marten	*Martes americana*
Fisher	*Martes pennanti*
Wolverine	*Gulo gulo*
Badger	*Taxidea taxus*
Least weasel	*Mustela nivalis*
Ermine	*Mustela erminea*
Long-tailed weasel	*Mustela frenata*
Black-footed ferret	*Mustela nigripes*
Western spotted skunk	*Spilogale gracilis*
Eastern spotted skunk	*Spilogale putorius*
Western hog-nosed skunk	*Conepatus mesoleucus*
Eastern hog-nosed skunk	*Conepatus leuconotus*
Striped skunk	*Mephitis mephitis*
Hooded skunk	*Mephitis macroura*
Ungulates	
Moose	*Alces alces*
Elk	*Cervus elaphus*
Mule deer	*Odocoileus hemionus*
White-tailed deer	*Odocoileus virginianus*
Musk ox	*Ovibos moschatus*
Caribou	*Rangifer tarandus*
Mountain goat	*Oreamnos americanus*
Dall's sheep	*Ovis dalli*
Bighorn sheep	*Ovis canadensis*
Pronghorn	*Antilocapra americana*
Collared peccary	*Pecari tajacu*

instances led to localized extinctions (Robinson and Bennett 2000). Similar results were found in North America. Mattson and Merrill (2002) analyzed relationships between landscape parameters, human influence, and persistence of grizzly bears, and determined that humans were a major factor in the decline of the grizzly bear range. Even before widespread European settlement in North America, humans had an influence on wildlife abundance and distribution (Hickerson 1965, Martin and Szuter 1999, Laliberte and Ripple 2003). Not all biomes have been affected by humans in the same way. For example, in North America, temperate grasslands have experienced a considerable quantitative decline resulting from conversion to agriculture (White et al. 2000), as well as a qualitative decline resulting from degradation and species losses (Noss et al. 1995). Therefore, it is important to examine human influences on wildlife in different biomes and to link human influences with species richness.

The purpose of this study was to compare historic and current species ranges and to identify large-scale patterns in range contractions and expansions. Our objectives were (a) to determine the degree of human influence on species range changes, (b) to compare the changes between historical and current species ranges with regard to biome and elevation, and (c) to describe changes in species richness. We hypothesized that human influence was positively associated with areas of species range contractions and negatively associated with areas of species persistence. Descriptive statistics and maps were used to show changes that occurred in species ranges with regard to biome and elevation.

Species, study area, and input variables

The study area comprised Canada, the United States, and Mexico. Our source for historic species ranges was *The Mammals of North America,* by Hall and Kelson (1959), whose maps are based on actual field sightings dating back to the 18th and 19th centuries. The maps represent the species' distributions before spatially extensive land transformation following Euro-American settlement, and they take into account the existing influence of North American aboriginal people. Map sources for current species ranges were digital versions of maps from *The Smithsonian Book of North American Mammals* (Wilson and Ruff 1999) and *Mammals of North America* (Kays and Wilson 2002).

We used ArcGIS software (ESRI 1999) to digitize the historic and current range maps for 32 carnivores and 11 ungulates (table 1) and to conduct further spatial analysis. We did not include the bison in our species list, because it had lost 99% of its historic range by 1889 (Hornaday 1889), and today most bison exist only in parks and reserves (Boyd 2003). Tropical cats were also not included. The current range maps for ocelot *(Leopardus pardalis)* and jaguarundi *(Puma yagouaroundi)* in our source (Kays and Wilson 2002) showed only parts of Mexico, and no current range maps were included for margay *(Leopardus wiedii)* or jaguar *(Panthera onca)*. The last record of a margay in Texas was from 1852, and the jaguar has been considered extinct in the United States, although there were some recent sightings in Arizona (Kays and Wilson 2002). The current range maps do not include all recent reintroductions of species, such as wolves in the northern Rocky Mountains of the United States.

Other digital input data included a map of the "human footprint" (Sanderson et al. 2002), a map of North American biomes (Olson et al. 2001), and a digital elevation model of North America (LPDAAC 2002) (figure 1). The human footprint map was created by incorporating four types of data representing human influence: (1) population density, (2) land transformation, (3) accessibility by roads and rivers, and (4) electrical power infrastructure. Electrical infrastructure as measured by nighttime lights visible from a satellite image has been correlated with population density (Sutton et al. 1997). The result of incorporating those four variables is a map showing the human influence index, ranging from 0 (low influence) to 100 (high influence).

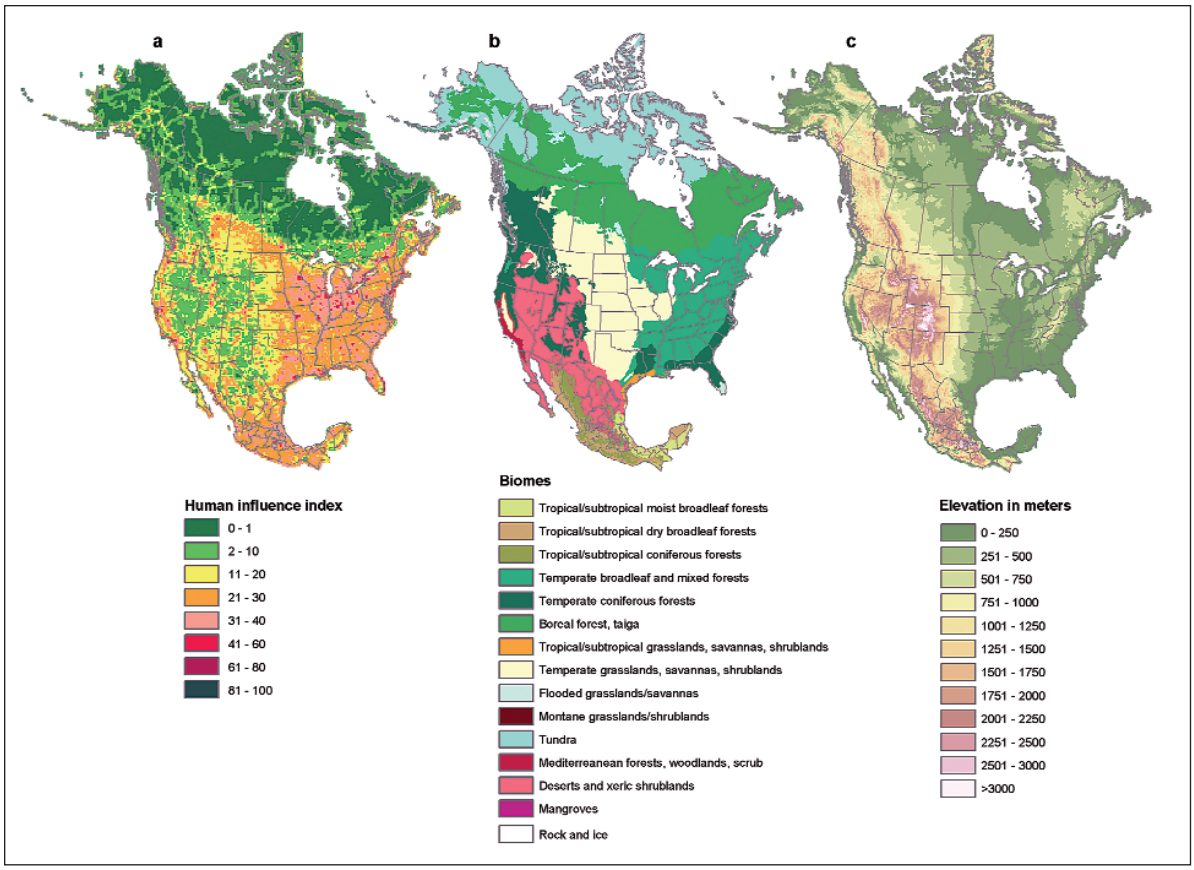

Figure 1. Shown are the input data used in the analysis. (a) Human footprint map depicting the human influence index, ranging from 0 (low) to 100 (high). The map is based on population density, accessibility, land transformation, and satellite nighttime lights (Sanderson et al. 2002). (b) Biomes of North America (Olson et al. 2001). (c) Digital elevation model of North America (LPDAAC 2002).

We chose the human footprint for assessing human influence on species range changes, because this map has several advantages over a map showing only human population density. First, it is still not known to what extent population density correlates with overall human influence (Sanderson et al. 2002). Second, land transformation and the resulting habitat loss and fragmentation represent one of the greatest threats to biodiversity (Vitousek et al. 1997, Wilcove et al. 1998). Third, roads are known to have a negative effect on ecological integrity, affecting species composition, animal population size, and various ecological processes (Trombulak and Frissell 2000). For those reasons, the human footprint map is well suited for our purpose. However, we recognize that some aspects of human influence that contribute to species range contractions may not be captured in the human influence index (e.g., trapping, predator poisoning, disease transmission from domestic livestock to wildlife, and livestock grazing).

The creators of the human footprint map stated that "we expect that where human influence is highest, ecosystems will be most modified and species under the most pressure from human activity" (Sanderson et al. 2002). We tested this hypothesis with regard to species range changes.

Potential error sources

There are certain problems associated with delineating geographic ranges of species. Many maps depict only outlines, omit holes in the ranges, or do not show islands along the perimeter. Maps of historic ranges usually include all locations where a species has been found in the past as well as areas that have been colonized relatively recently (Brown et al. 1996). In addition, species are not evenly distributed throughout their habitat (Brown 1984), and information on species density is not portrayed in maps showing geographic range. Other problems with studying range maps are the use of different spatial scales, the fact that there are many techniques to measure the range size of a species, and the difference between extent of occurrence and area of occupancy (Gaston 1996). Finally, range maps are not updated frequently but may still appear in reference works as depicting the current range of a species.

A map can depict only a snapshot in time, and different mapmakers often display slightly different ranges for the same species. After comparing several sources for range maps of the same species, we came to the conclusion that it was difficult to find complete agreement about exact range boundaries. For those reasons and for the sake of consistency, we de-

cided it was important to use maps from the same source for each time period chosen. We caution that the range boundaries are not set in stone and that they should be considered to be fuzzy rather than distinct. It is also assumed that not all areas within a species' geographic range are occupied. We are aware that species ranges are dynamic and that there may have been contractions and expansions between the two time periods we considered. We stress that this study was conducted on a relatively coarse scale and that we examined broad changes. Our maps were not designed to be used and interpreted at a finer scale than the one used in our study.

Range contractions, expansions, and areas of persistence

The historic and current ranges of each species were overlaid in the geographic information system (GIS) to determine areas of range contraction, expansion, and persistence for the 43 species. In general, large carnivores and ungulates experienced considerable loss of area compared with their historic range (table 2). However, species well adapted to live close to humans, such as the raccoon and coyote, showed range expansions (18% and 40%, respectively).

Because we wanted to determine the degree of human influence on species range changes, we were concerned about potential error sources in the data. Most species that underwent range contractions also showed areas of expansion, which led us to scrutinize the maps in greater detail. As we already discussed, it was assumed that species range maps were not always entirely accurate. We were especially skeptical about small slivers of expansion areas around the edges of the range of those species that had experienced large degrees of range contractions. We assumed that those differences could be attributed at least in part to the different map sources. After closely examining the areas of contraction, expansion, and persistence of each species, we decided to use a threshold value that would represent a safe margin of error. We decided to analyze the relationship between range contractions and human influence for only those species that had experienced range contractions over more than 20% of their historic range (table 2). (We did not analyze that relationship for the black-footed ferret, however, because its historic range contracted 100%, leaving no area of persistence.) We acknowledge that this threshold was picked subjectively on the basis of our belief that it would account at least in part for the inaccuracies in the original maps and for potential

Table 2. Percentage contraction, expansion, persistence, and net loss or increase of areas for 43 North American carnivores and ungulates.

Species	Area of contraction	Area of expansion	Area of persistence	Area of net loss (–) or increase (+)
Contractions of more than 20%				
Black-footed ferret	100	0	0	–100
Elk	77	3	23	–74
Pronghorn	64	0	36	–64
Swift fox	68	8	32	–60
Dall's sheep	64	10	36	–54
Grizzly bear	55	2	45	–53
Fisher	50	3	50	–47
Gray wolf	42	0	58	–42
Lynx	40	1	60	–39
Black bear	41	2	59	–39
Wolverine	39	2	61	–37
Cougar	40	4	60	–36
Musk ox	35	4	65	–31
Mountain goat	43	12	57	–31
River otter	25	0	75	–25
Bighorn sheep	40	15	60	–25
Caribou	24	0	76	–24
Marten	21	2	79	–19
Contractions of less than 20%				
American mink	13	1	87	–12
Moose	15	4	85	–11
Mule deer	14	6	86	–8
Polar bear	6	0	94	–6
Arctic fox	10	5	90	–5
Bobcat	10	5	90	–5
Long-tailed weasel	0	0	100	0
Eastern hog-nosed skunk	0	0	100	0
Collared peccary	0	0	100	0
Western hog-nosed skunk	3	4	97	+1
Striped skunk	1	1	99	+1[a]
Ermine	0	1	100	+1
Eastern spotted skunk	9	11	91	+2
Ringtail	5	7	95	+2
White-nosed coati	2	5	98	+2[a]
Gray fox	3	8	97	+5
White-tailed deer	1	7	99	+6
Western spotted skunk	4	10	96	+6
Least weasel	0	8	100	+8
Hooded skunk	1	11	99	+10
Red fox	4	17	96	+13
Kit fox	12	28	88	+16
Badger	1	18	99	+17
Raccoon	0	18	100	+18
Coyote	0	40	100	+40

Note: Areas of contraction, expansion, and persistence are expressed as a percentage of the species' historic range. Net loss or net increase is the difference between the percentage area of the contraction and percentage area of expansion. Species are sorted from largest net loss to largest net increase.

a. Because of rounding, the difference in percentage area of contraction and percentage area of expansion does not equal the figure shown as percentage area of net loss or increase.

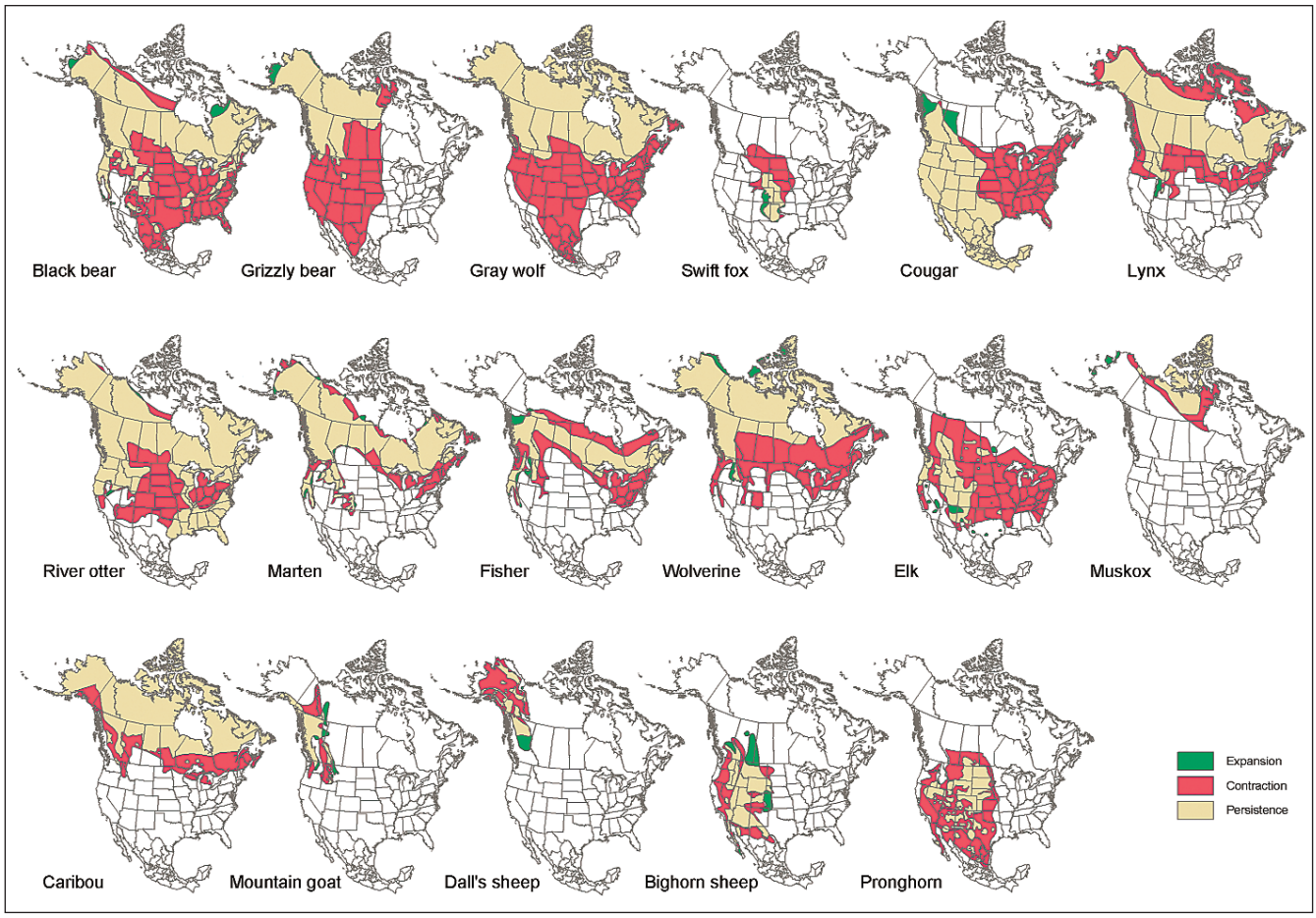

Figure 2. Areas of expansion, contraction, and persistence, based on historic and current species ranges for 17 species that experienced range contractions over more than 20% of their historic range.

digitizing errors. Moreover, we believed that using this threshold would represent a conservative approach yet still ensure that species with large range changes would be incorporated in the analysis.

The range changes for 17 species with range contractions over more than 20% of their historic range are shown in figure 2. Large carnivores (black bear, grizzly bear, gray wolf, cougar, and wolverine) all lost considerable portions of their historic range. A potential effect of range contractions of large carnivores is a mesopredator release (Soulé and Terborgh 1999), the increase and resulting overabundance of small to midsize predators. In fact, our study showed that the ranges of smaller predators (e.g., coyotes and raccoons) expanded from historical times (table 2). Concern is growing over the importance of large carnivore conservation because of the cascading effects of predators on lower trophic levels (Terborgh et al. 1999) and the loss of species interactions leading to simplified or degraded ecosystems (Soulé et al. 2003). Vegetation communities can be profoundly diminished by ungulates when top predators (wolves, e.g.) are removed from an ecosystem (Ripple and Larsen 2000).

It appears that 12 of the 17 species contracted toward the edge of their historic range, while 5 species (lynx, marten, fisher, bighorn sheep, and pronghorn) appear to have contracted more toward the center of their historic range. A contraction toward the north was especially noticeable for species whose historic range covered a large part of North America (i.e., black bear, grizzly bear, gray wolf, and wolverine). Other researchers (Lawton et al. 1994, Channell and Lomolino 2000a) have analyzed patterns of range contractions in more detail. We focused on determining the degree of human influence on range dynamics.

Assessing human influence on species range changes

We hypothesized that a species was more likely to persist in areas of lower human influence and more likely to contract in areas of higher human influence. We applied the human footprint map to areas of persistence and contraction, although the map was compiled from recent information, thereby being more correlated to persistence than to contraction. In applying the human footprint map to areas of contraction, we assumed that human encroachment and impacts had occurred over time, just as animal contractions had. This applies especially to land conversions. For example, from 1860 to 1920, North American land converted to crop-

land increased from 25,000 square kilometers (km^2) to 1.6 million km^2 (Richards 1984). On the other hand, despite the general trend of human encroachment over time, the human footprint probably decreased in some areas. Examples include newly created wilderness areas, ecological restoration efforts, and nature reserves. We emphasize that these fluctuations of the human footprint exist, but they cannot be captured easily, considering that the study has a relatively coarse scale and represents a snapshot of historic and current conditions.

Using the GIS software, we clipped the species' areas of contraction and persistence out of the human footprint map and calculated the proportional areas in each of the eight human influence index classes. We then calculated an electivity index for each human influence index class in areas of contraction and areas of persistence to compare occupied with available range. We used Ivlev's electivity index (Ivlev 1961), which compares the proportion of area used by the species to the proportion of area available. Ivlev's electivity index ranges from –1 to +1; negative values suggest avoidance (or lower concentration than chance alone would be expected to produce), positive values suggest preference of the resource (or higher concentration than chance alone would be expected to produce), and 0 indicates a neutral response (or a proportion equal to availability) (Manly et al. 1993). The proportion of area used corresponded to the proportional area in each human influence class, while the proportion available was the proportion of the combined areas of persistence and contraction in the same human influence class. Bonferroni confidence intervals were constructed to determine whether preference or avoidance was statistically significant ($P < 0.01$). A hypothesis of no preference or avoidance of the proportional range in each human influence class cannot be rejected if the Bonferroni confidence interval includes the proportion available (White and Garrott 1990).

For nearly all species, electivity values for areas of persistence decreased with increasing human influence index (figure 3), indicating that those species were less likely to persist in areas of higher human influence. Species exhibiting this trend also showed a high electivity value in the lowest human influence index class. This suggests that these species were more likely to persist in areas of low human influence. In contrast, the areas of contraction were mirror images of the areas of persistence, with species more likely to contract in areas of higher human influence and less likely to contract in areas of lower human influence.

Species that showed a pronounced trend for persistence in areas of lower human influence had electivity values closer to –1 than to 0; among these were grizzly bear, gray wolf, marten, wolverine, musk ox, and caribou, species associated with sensitivity to human disturbance. The highest electivity values for areas of contraction were close to 0.5 and were exhibited by the same species. Although electivity values for the remaining species were lower, most of them showed the same trend: For areas of persistence, electivity values decreased with increasing human influence, and for areas of contraction, electivity values increased with increasing human influence. This shows that the majority of the species examined displayed some degree of response to human influence.

The lines for contraction and persistence tended to converge at 0 electivity in the human influence index class 2–10 (figure 3). This indicates that species were found in this human influence class at a concentration close to the expected availability. It appears that areas with a human influence index of 2 to 10 were not strongly associated with either contraction or persistence of most species. It follows that those locations represent areas where humans have little or no influence on range contractions. In North America, areas with a human influence index of 2 to 10 are found predominantly in Canada, Alaska, and parts of the western United States (figure 1).

A comparison of the human influence map (figure 1) and the map of the species' range changes (figure 2) clarifies some of the responses shown in the electivity graphs, because many species (gray wolf, grizzly bear, black bear, elk, cougar, and wolverine) lost a large part of their range in areas of higher human influence. The pronghorn did not show strong responses to human influence, although it lost 64% of its historic range. The relationship with human influence was assumed to be weak for pronghorn, because the historic and current ranges were comparable in terms of the human influence index. Pronghorn contracted toward the center of their historic range, while species such as the grizzly bear and gray wolf contracted toward the north, an area considerably lower in human influence.

Dall's sheep, bighorn sheep, and mountain goats also did not display very strong responses to human influence. We assume this is because the historic as well as the current ranges of those species were located in areas of relatively low human influence (western United States, Canada, and Alaska). This can be verified by comparing the human influence map with the maps of species' range change.

Changes within biomes

Because of the large changes observed between historic and current species ranges, it was expected that some species might not be found today in biomes that they had occupied historically. We were interested in documenting the changes between historic and current species ranges by biome, because this information is applicable to wildlife conservation and species reintroductions. For all of the 17 species, we summarized the historical and current ranges by biome and calculated the percentage of the historic range lost by biome (table 3). The results show not only how much area was lost in each biome but also how the biome composition of the range changed over time. Some species lost more than 50% of their historic range, while the biome composition of their range did not change much. For example, the pronghorn lost 55% to 68% of its historic range in the three biomes it occupied. However, the proportion of each biome in the historic or current range remained similar. A look at the pronghorn range contraction map (figure 2) shows a spatial representation of those changes. Although it is known that pronghorn occur

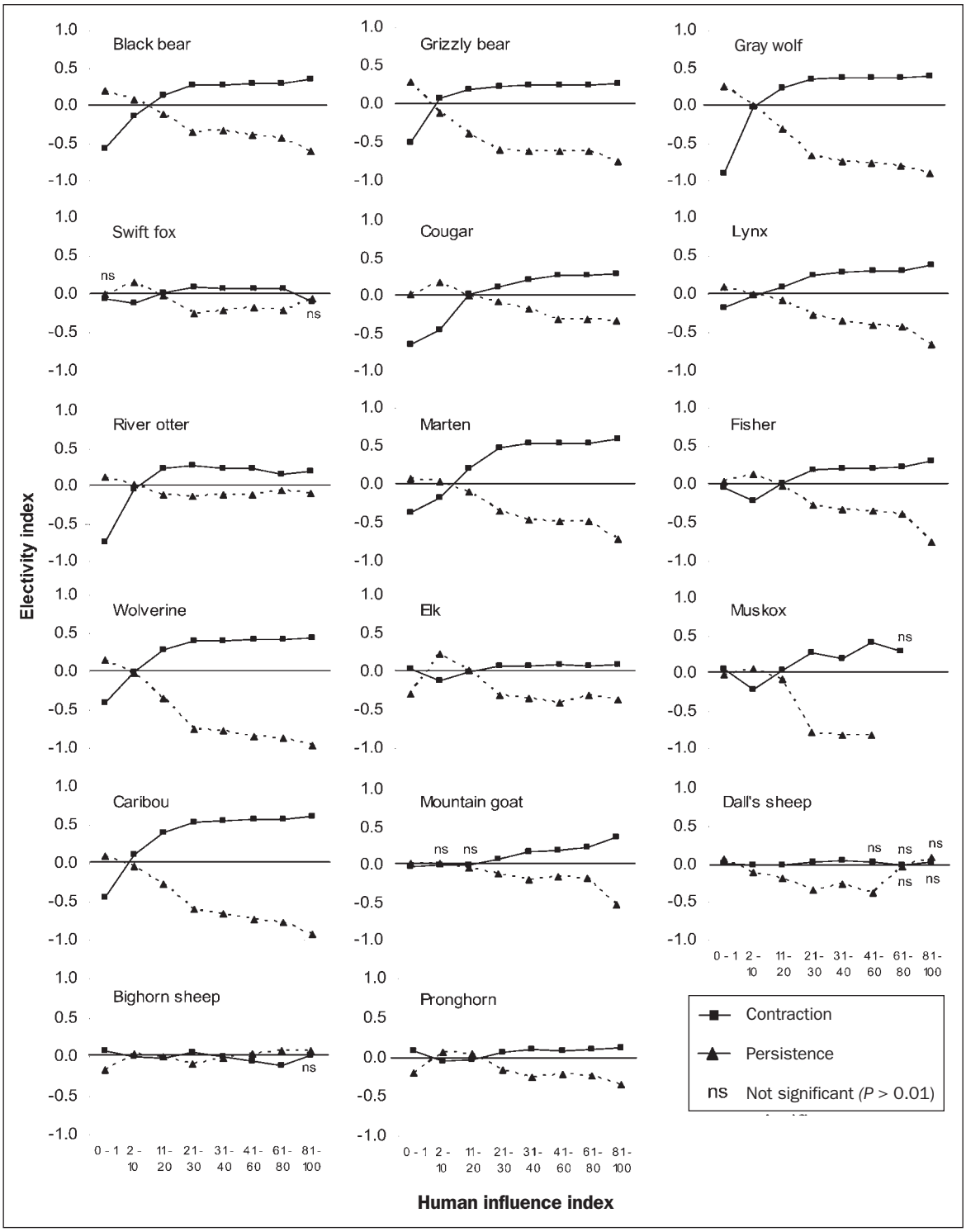

Figure 3. Electivity index graphs for 17 species that experienced range contractions over more than 20% of their historic range. Electivity indexes are shown for areas of contraction and persistence for each species in each of eight human influence index classes (x-*axis). Ivlev's electivity index is calculated as* $(P_u - P_a)/(P_u + P_a)$*, where* P_u *is the proportion of area used by the species and* P_a *is the proportion of area available. The index ranges from –1 to +1; negative values suggest avoidance (or lower concentration than expected by chance alone), positive values suggest preference of the resource (or higher concentration than expected by chance alone), and 0 indicates a neutral response (or a proportion equal to availability). Bonferroni confidence intervals* (P *< 0.01) were constructed to determine whether preference or avoidance was statistically significant. A hypothesis of no preference or avoidance of the proportional range in each human influence class cannot be rejected if the Bonferroni confidence interval includes the availability proportion.*

Table 3. Area of species' historic and current ranges and percentage of historic range lost, summarized by biome.

Species	Biome	Area in thousands of square kilometers		Area as percentage of total		Percentage of historic range lost
		Historic	Current	Historic	Current	
Black bear	Temperate broadleaf mixed forests	2807	1396	18	15	50
	Temperate coniferous forests	2252	1638	14	17	27
	Boreal forests/taiga	4846	4750	31	50	2
	Temperate grasslands, savannas, and shrublands	3039	392	19	4	87
	Tundra	1079	865	7	9	20
	Deserts and xeric shrublands	1361	327	9	3	76
	Other	396	120	3	1	70
	Total	15,780	9488			40
Grizzly bear	Temperate coniferous forests	1690	797	5	16	53
	Boreal forests/taiga	2771	2160	25	42	22
	Temperate grasslands, savannas, and shrublands	2293	212	21	4	91
	Tundra	2075	1909	19	37	8
	Deserts and xeric shrublands	1778	1	16	0	100
	Other	408	54	4	1	87
	Total	11,015	5133			53
Gray wolf	Temperate broadleaf mixed forests	2296	503	13	5	78
	Temperate coniferous forests	1850	831	10	8	55
	Boreal forests/taiga	5071	4884	28	47	4
	Temperate grasslands, savannas, and shrublands	2965	438	16	4	85
	Tundra	3704	3681	20	35	1
	Deserts and xeric shrublands	1942	1	11	0	10
	Other	492	163	3	2	67
	Total	18,320	10,501			43
Swift fox	Temperate coniferous forests	50	63	3	9	[25]
	Temperate grasslands, savannas, and shrublands	1621	597	91	84	63
	Deserts and xeric shrublands	106	51	6	7	51
	Total	1777	711			60
Cougar	Tropical/subtropical coniferous forests	473	473	4	7	0
	Temperate broadleaf mixed forests	2565	66	23	1	97
	Temperate coniferous forests	2072	1716	19	25	17
	Temperate grasslands, savannas, and shrublands	2514	1294	23	19	49
	Deserts and xeric shrublands	2329	2329	21	34	0
	Other	998	1063	9	15	[7]
	Total	10,951	6941			37
Lynx	Temperate broadleaf mixed forests	1712	770	13	10	55
	Temperate coniferous forests	1417	859	11	11	39
	Boreal forests/taiga	5068	4712	38	59	7
	Temperate grasslands, savannas, and shrublands	1609	441	12	5	73
	Deserts and xeric shrublands	2983	1065	23	13	64
	Other	396	197	3	2	50
	Total	13,185	8044			39
River otter	Temperate broadleaf mixed forests	2813	2102	18	18	25
	Temperate coniferous forests	2222	1941	14	17	13
	Boreal forests/taiga	5062	4963	33	43	2
	Temperate grasslands, savannas, and shrublands	2861	637	19	5	78
	Tundra	1546	1499	10	13	3
	Deserts and xeric shrublands	768	339	5	3	56
	Other	170	150	1	1	12
	Total	15,442	11,631			25
Marten	Temperate broadleaf mixed forests	1361	535	15	7	61
	Temperate coniferous forests	1453	1255	16	17	14
	Boreal forests/taiga	4818	4468	52	60	7
	Tundra	1041	886	11	12	15
	Other	593	353	6	5	40
	Total	9266	7497			19
Fisher	Temperate broadleaf mixed forests	1858	820	29	24	56
	Temperate coniferous forests	1194	847	19	25	29
	Boreal forests/taiga	2660	1554	42	45	42
	Temperate grasslands, savannas, and shrublands	548	129	9	4	77
	Other	149	78	2	2	48
	Total	6409	3428			47

mainly in grasslands and shrublands (Yoakum and O'Gara 2000), our analysis showed that the pronghorn's range included temperate coniferous forests. We assume that this biome for pronghorn may be overestimated because of map scale and imprecision and because not all areas in a species' geographic range are occupied. However, the historic range map by Hall and Kelson (1959) contains at least 11 marginal records that fall within the temperate coniferous forest biome, which indicates that pronghorn may have historically occupied smaller grassland areas within this biome.

Other species lost portions of their historic range, and the biome composition of their range also underwent large changes. The grizzly bear's historic and current ranges show very different biome structures: Historically, the temperate grasslands contributed 21% to the entire range, whereas currently only 4% of the entire range is in this biome. The grizzly also lost all of its range in the desert and xeric shrublands, which historically contributed 16% to the total. The gray wolf showed a response similar to that of the grizzly bear. Both species lost all of their historic ranges in the desert and xeric

Table 3 *(continued)*

Species	Biome	Area in thousands of square kilometers		Area as percentage of total		Percentage of historic range lost
		Historic	Current	Historic	Current	
Wolverine	Temperate broadleaf mixed forests	1356	0	11	0	100
	Temperate coniferous forests	1450	742	11	9	49
	Boreal forests/taiga	5037	3410	39	42	32
	Temperate grasslands, savannas, and shrublands	1158	69	9	1	94
	Tundra	3466	3703	27	46	[7]
	Other	330	191	3	2	42
	Total	12,797	8115			37
Elk	Temperate broadleaf mixed forests	1889	43	23	2	98
	Temperate coniferous forests	1493	1026	19	49	31
	Boreal forests/taiga	980	82	12	42	92
	Temperate grasslands, savannas, and shrublands	2825	289	35	14	90
	Deserts and xeric shrublands	827	662	10	31	20
	Other	51	6	1	0	89
	Total	8065	2108			74
Musk ox	Boreal forests/taiga	444	131	19	8	70
	Tundra	1742	1341	76	85	23
	Rock and ice	112	112	5	7	0
	Total	2298	1584			31
Caribou	Temperate broadleaf mixed forests	870	0	8	0	100
	Temperate coniferous forests	662	235	6	3	64
	Boreal forests/taiga	5051	4324	47	53	14
	Tundra	3656	3435	34	42	6
	Other	505	208	5	3	59
	Total	10,744	8202			24
Mountain goat	Temperate coniferous forests	728	480	50	47	34
	Boreal forests/taiga	395	320	27	2	19
	Tundra	267	127	18	13	52
	Other	71	87	5	9	[23]
	Total	1461	1014			31
Dall's sheep	Temperate coniferous forests	69	208	4	25	[203]
	Boreal forests/taiga	753	252	43	31	67
	Tundra	905	342	51	41	62
	Other	34	23	2	3	31
	Total	1761	825			53
Bighorn sheep	Temperate coniferous forests	1041	630	32	26	39
	Temperate grasslands, savannas, and shrublands	467	704	14	29	[51]
	Deserts and xeric shrublands	1638	1053	50	43	36
	Other	116	65	4	3	44
	Total	3262	2452			25
Pronghorn	Temperate coniferous forests	613	225	11	11	63
	Temperate grasslands, savannas, and shrublands	2352	1057	43	53	55
	Deserts and xeric shrublands	2156	700	39	35	68
	Other	348	23	6	1	93
	Total	5469	2005			63

Note: The 17 species in this table experienced range contractions over more than 20% of their historic range. The "other" category includes biomes that encompassed less than 5% of total historic or current range. Percentage totals may not equal 100 because of rounding. Numbers in brackets include percentage increase over historic range.

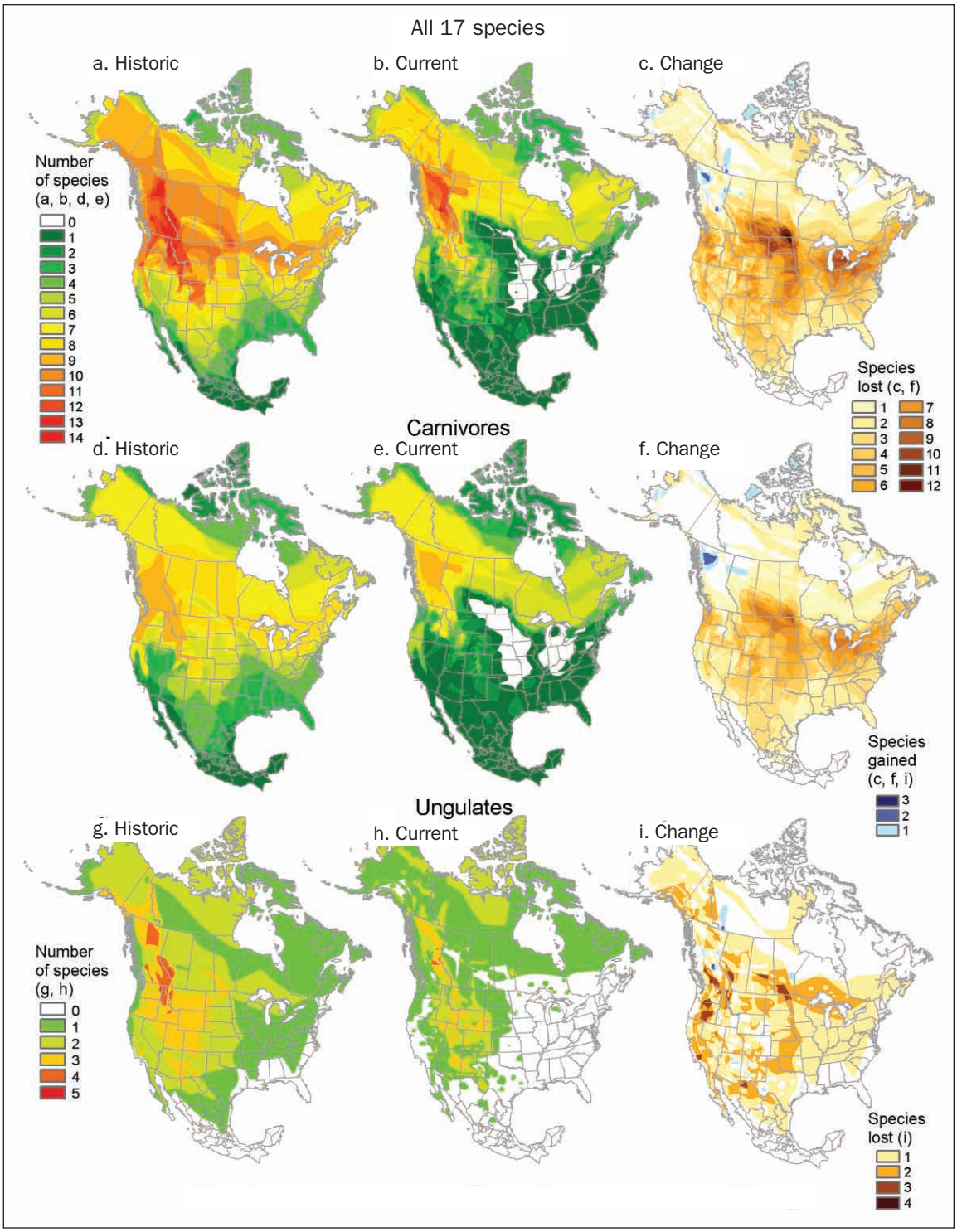

Figure 4. Historic and current species richness and number of species lost over time for 17 species that experienced range contractions over more than 20% of their historic range (a, b, c), for 10 carnivores (d, e, f), and for 7 ungulates (g, h, i). The maps for historic and current species richness were created by combining the historic or current range maps for the species. The maps showing the number of species lost or gained over time were created by subtracting the current from the historic maps.

Table 4. Area of species' historic and current ranges and percentage of historic range lost, summarized by five elevation classes.

Species	Elevation	Area in thousands of square kilometers		Area as percentage of total		Percentage of historic range lost
		Historic	Current	Historic	Current	
Black bear	0–500	8912	5611	56	58	37
	501–1000	3233	1889	20	20	42
	1001–1500	1773	942	11	10	47
	1501–2000	1162	639	7	7	45
	> 2000	838	519	5	5	38
	Total	15,918	9600			40
Grizzly bear	0–500	4294	2787	39	54	35
	501–1000	2772	1207	25	23	56
	1001–1500	1902	719	17	14	62
	1501–2000	1303	360	12	7	72
	> 2000	863	133	8	3	85
	Total	11,134	5206			53
Gray wolf	0–500	10,559	7237	57	68	31
	501–1000	3541	2070	19	19	42
	1001–1500	1973	840	11	8	57
	1501–2000	1420	385	8	4	73
	> 2000	987	105	5	1	89
	Total	18,480	10,637			42
Swift fox	0–500	280	10	16	1	96
	501–1000	886	209	50	29	76
	1001–1500	400	297	23	42	26
	1501–2000	109	117	6	16	[7]
	> 2000	101	78	6	11	23
	Total	1776	711			60
Cougar	0–500	5100	1478	47	21	71
	501–1000	1890	1443	17	21	24
	1001–1500	1632	1639	15	24	0
	1501–2000	1308	1357	12	20	[4]
	> 2000	1029	1033	9	15	0
	Total	10,959	6950			37
Lynx	0–500	8506	5019	64	61	41
	501–1000	2757	1756	21	22	36
	1001–1500	1078	761	8	9	29
	1501–2000	591	432	4	5	27
	> 2000	403	195	3	2	52
	Total	13,335	8163			39
River otter	0–500	9524	7804	61	66	18
	501–1000	3098	2027	20	17	35
	1001–1500	1380	1015	9	9	26
	1501–2000	932	613	6	5	34
	> 2000	648	303	4	3	53
	Total	15,582	11,762			25
Marten	0–500	5784	4338	62	57	25
	501–1000	1821	1619	19	21	11
	1001–1500	836	809	9	11	3
	1501–2000	525	495	6	7	6
	> 2000	430	323	5	4	25
	Total	9396	7584			19
Fisher	0–500	4268	2146	66	62	50
	501–1000	1245	645	19	19	48
	1001–1500	462	352	7	10	24
	1501–2000	315	226	5	7	28
	> 2000	199	98	3	3	51
	Total	6489	3467			47
Wolverine	0–500	8342	5558	64	68	33
	501–1000	2654	1508	20	18	43
	1001–1500	988	738	8	9	25
	1501–2000	552	347	4	4	37
	> 2000	416	82	3	1	80
	Total	12,952	8233			36

Table 4 (continued)

Species	Elevation	Area in thousands of square kilometers: Historic	Area in thousands of square kilometers: Current	Area as percentage of total: Historic	Area as percentage of total: Current	Percentage of historic range lost
Elk	0–500	3705	273	46	13	93
	501–1000	1972	285	24	14	86
	1001–1500	1053	438	13	21	58
	1501–2000	755	537	9	25	29
	> 2000	620	575	8	27	7
	Total	8105	2108			74
Musk ox	0–500	2096	1381	90	87	34
	501–1000	164	148	7	9	10
	1001–1500	49	47	2	3	4
	1501–2000	18	17	1	1	1
	> 2000	1	1	0	0	0
	Total	2328	1594			32
Caribou	0–500	7804	6223	72	75	20
	501–1000	1933	1408	18	17	27
	1001–1500	719	457	7	5	37
	1501–2000	339	195	3	2	42
	> 2000	92	28	1	0	70
	Total	10,887	8311			24
Mountain goat	0–500	151	144	10	14	5
	501–1000	359	280	25	27	22
	1001–1500	493	298	34	29	39
	1501–2000	329	206	23	20	37
	> 2000	131	89	9	9	32
	Total	1463	1017			31
Dall's sheep	0–500	635	68	36	8	89
	501–1000	522	308	30	37	41
	1001–1500	375	285	21	34	24
	1501–2000	191	141	11	17	26
	> 2000	42	24	2	3	42
	Total	1765	826			53
Bighorn sheep	0–500	222	157	7	6	29
	501–1000	557	563	17	23	[1]
	1001–1500	925	686	28	28	26
	1501–2000	862	598	26	24	31
	> 2000	697	448	21	18	36
	Total	3263	2452			25
Pronghorn	0–500	1152	142	21	7	88
	501–1000	1471	644	27	32	56
	1001–1500	1168	516	21	26	56
	1501–2000	953	386	17	19	59
	> 2000	725	318	13	16	56
	Total	5469	2006			63

Note: Included are 17 species experiencing range contractions over more than 20% of their historic range. Percentage totals may not equal 100 because of rounding. Numbers in brackets indicate percentage increase over historic range.

shrublands; both lost large portions in the grasslands; and proportionally both now have more range in the boreal forest and tundra. Although wolves and grizzlies were probably never as common in the desert and xeric shrublands as in other biomes they occupied, wolves are thought to have occupied all habitats that supported ungulate populations (Ballard and Gipson 2000). In addition, marginal records in the distribution maps by Hall and Kelson (1959) show several locations where grizzly bears and wolves were recorded in the desert and xeric shrubland, although it is possible that those sites are in riparian areas and in close proximity to mountain ranges where sufficient food resources could be found. The decline of grizzlies in the Great Plains has been associated with the decline of bison, one of their main food sources in that biome (Mattson and Merrill 2002). Large herds of elk, pronghorn, and deer were also reduced on the plains. We presume that the decline of these prey led to the loss of their main predators, the wolves and grizzlies. In addition, humans exterminated many predators.

We believe that there is cause for concern if a species experiences a loss of its historic range and if the historic and current range structures also differ considerably. The former would lead to a general loss of populations; the latter could result in the extinction of certain subspecies adapted to particular biomes. In addition to a decrease or loss in areal extent, degradation of a biome has to be considered in determining the extent of range contractions. For example, relatively little of the sagebrush steppe has been converted to

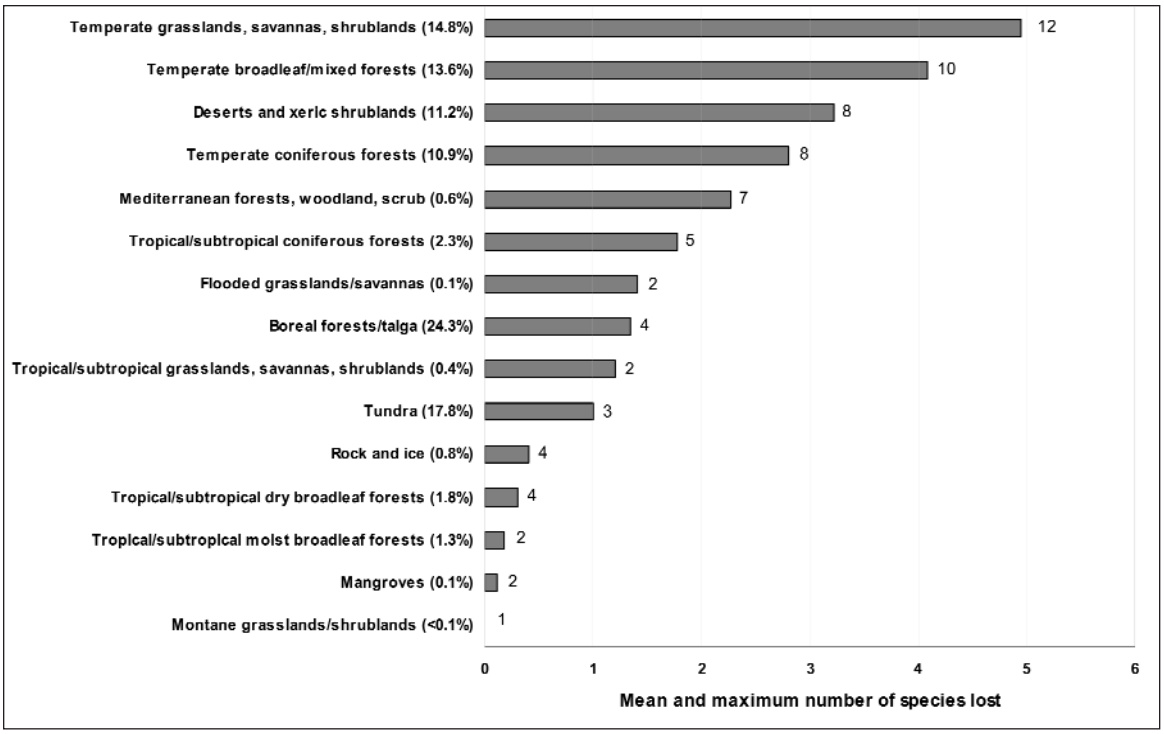

Figure 5. Mean and maximum number of species lost in each biome. Bars indicate means, and numbers following bars indicate maxima. Means were calculated by weighting the number of species lost in each biome by the proportional area each occupied in that biome. The proportion of North American land that each biome constitutes is shown as a percentage after the biome's name.

urban areas, but 95% has been affected by various influences, such as exotic plant invasion, altered fire regimes, and livestock grazing (Noss et al. 1995).

We also observed increases in the current range compared with the historic range. Dall's sheep, for example, apparently experienced an increase in the temperate coniferous forest, specifically in the north-central part of British Columbia. A subspecies of Dall's sheep, the stone sheep *(Ovis dalli stonei),* lives in this area, which supports most of the world's population of stone sheep. Although the range of the stone sheep extends southward to north-central British Columbia, the largest population is found in the northern portion of the province, with fewer individuals living near the southern boundary of the current range (MELP 2000). This information suggests that the current range of Dall's sheep does not extend quite as far south as shown. Therefore, the increase in range demonstrates a potential problem associated with outlining species ranges and thus should be interpreted with caution. Likewise, the bighorn sheep showed an increase in the temperate grasslands, mainly in Alberta. Again, we believe that the map boundaries probably extend too far into the eastern part of Alberta, since bighorn sheep are found mostly in mountainous regions (Krausman and Shackleton 2000).

The swift fox showed an increase in the temperate coniferous forest, but historically this biome contributed only 3% to its entire range. We are also skeptical of this increase, since it lies around the boundary of the range and could be attributed to differences in map creation. Since we considered only the 17 species that had experienced areas of contractions of 20% or more, we would be equally cautious about interpreting overall expansions that were smaller than the 20% threshold, as shown for Dall's sheep (10%), bighorn sheep (15%), and swift fox (8%) (table 2).

Changes within elevation zones

We summarized changes between historic and current ranges by species and elevation classes as well (table 4). Again, we observed shifts in elevation classes and a general loss of the species' historic ranges. For example, cougar, elk, and Dall's sheep lost considerable areas in the lower elevations and shifted their ranges to the upper-elevation classes. Although the grizzly bear lost 35% of its historic range in the lowest elevation class, the proportion of that class is actually higher in the current than in the historic range. This is because of the large loss of high-elevation range, particularly in the United States, and a much smaller loss of low-elevation classes in Canada. The only remaining areas of grizzly bear range in the United States at an elevation above 2000 meters are in northwestern Wyoming, northwestern Montana, and northern Washington (figure 2).

Historic and current species richness

Aside from individual species responses, we were interested in investigating how species richness had changed over time.

In the GIS, we added the historic ranges and the current ranges for 17 species that had undergone range contractions over more than 20% of their historic range. This resulted in two maps showing how species richness had decreased and shifted over time (figure 4a, 4b). We repeated this process separately for carnivores (figure 4d, 4e) and ungulates (figure 4g, 4h). To visualize how many species were lost, we then subtracted the current from the historic species richness map for the 17 species (figure 4c), for carnivores (figure 4f), and for ungulates (figure 4i).

To a large degree, the results mirrored the human influence map (figure 1), with species losses generally occurring in areas of higher human influence. The northern part of the Rocky Mountains stood out as an area of higher species richness, both historically and currently. The impact of land conversion can also be seen on the species richness map. The temperate grassland biome was especially affected by species losses, and the carnivores examined in our study were almost completely absent from this biome in the current species richness map (figure 4e).

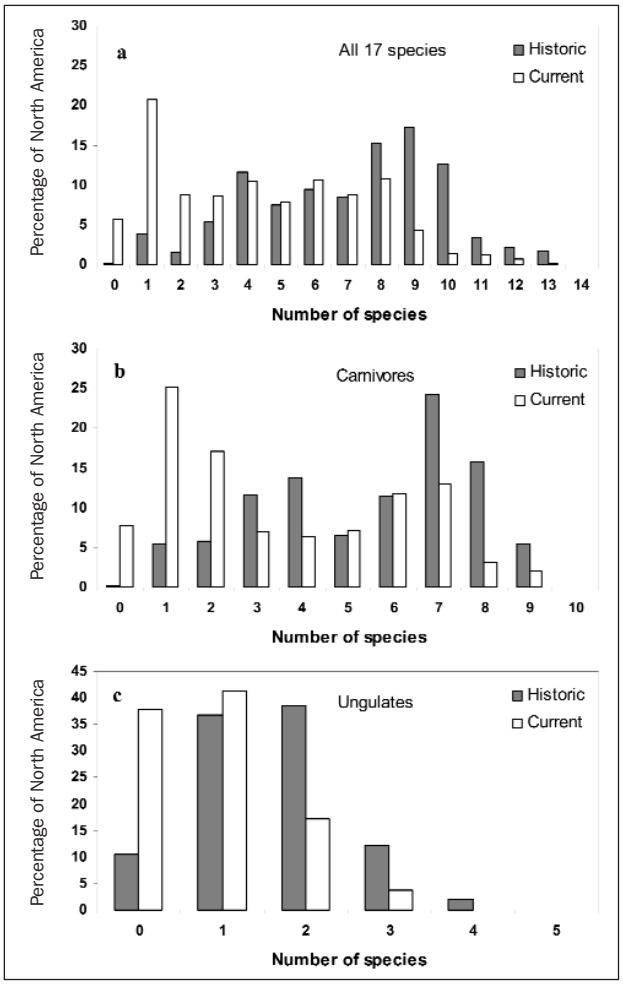

Figure 6. Percentage of North America occupied by number of species historically and currently (a) for all 17 species, (b) for carnivores, and (c) for ungulates (see also figure 4).

We calculated the average number of species lost in each biome by weighting the number of species lost by the proportional area over which a given number of species (one, two, three, etc.) were lost in that biome. The average number of species lost was highest for the temperate grasslands, savannas, and shrublands, where an average of five species were lost (figure 5). This is not surprising, because this biome has been converted extensively. Only 43% of the biome remains in native vegetation, while 41% has been converted to agriculture and 6% to urban areas (White et al. 2000).

The area with the highest number of species lost is located in southern Manitoba and northeastern North Dakota, in the tallgrass prairie, which is one of the most highly altered grasslands in the world (figure 4c; White et al. 2000). Only 9% of the original tallgrass prairie remains, while 71% has been converted to cropland and 18% to urban areas. Since 1830, the tallgrass prairie has decreased by 97%, and Manitoba and North Dakota have each lost more than 99% of this prairie type. Overall, the North American prairies have declined by an average of 79% since the early 1800s (White et al. 2000).

In addition to this quantitative decline, a qualitative decline has taken place. Noss and colleagues (1995) found that among ecosystems showing the greatest decline in terms of land conversion and degradation, grasslands and savannas experienced the greatest losses. This explains why the temperate grassland biome showed a high level of species loss. The removal of native vegetation followed by farming led to soil exposure and subsequent wind and water erosion. Addition of fertilizers and pesticides changed the soil composition and the moisture regime of the area. In addition, the fire regime of the former grassland was changed drastically. All of this affected the plants and, in turn, many animal species, which failed to survive or thrive in those areas.

In the temperate broadleaf, mixed forest biome, an average of four species were lost, which can be explained by the relatively high human population as well as land conversions from native to managed forests and agriculture in this biome. Deserts and xeric shrublands, and temperate coniferous forests, lost approximately three species on average. Biomes that lost a relatively low number of average species (approximately two species or fewer) included boreal forests and tundra, tropical and subtropical moist and dry broadleaf forests, and mangroves (figure 5).

Similarly, Hannah and colleagues (1995) determined that on a global scale, temperate biomes were more disturbed than tropical biomes, while in North America undisturbed grasslands were especially rare. However, this has to be interpreted with regard to the species we included in this study. Most of our species historically occupied the northern half of North America and later contracted to the northern portion of the continent (figure 2). We investigated few species that occupied a large portion of the tropical and subtropical biomes, such as tropical cats; therefore, our conclusions for those biomes are limited.

Historically, only 4% of North America was occupied by one species; that percentage has since risen to 21%. At the same time, the area occupied by nine species has decreased from 17% to 4%. In general, a larger proportion of North America was covered by a greater number of species historically than it is now. This result was seen for both carnivores and ungulates (figure 6). Ceballos and Ehrlich (2002) created similar global maps of mammal species losses and found that for 18 species in North America, the highest percentage losses were in the densely populated eastern United States. The differences in maps can be attributed to the fact that Ceballos and Ehrlich (2002) investigated different species, including several whose ranges were located further south.

Conclusions and recommendations

Human influence was definitely related to areas of contraction and persistence for nearly all of the species examined in this study. In areas of higher human influence, species were more likely to contract and less likely to persist. Species losses were greatest for the temperate grassland, savanna, and shrubland biome, an area that has undergone substantial land conversion from native vegetation to agricultural lands. It is not surprising that humans have influenced species range dynamics; however, little information was previously available on human influences on species range changes in North America. We greatly benefited from the use of the human footprint map (Sanderson et al. 2002) and the map of biomes (Olson et al. 2001), parts of a global data set that has only recently become available. As our maps show, species ranges cross regional and country boundaries, and it is imperative that conservation biologists apply data sets that cross the same boundaries. Political boundaries often hinder or limit conservation efforts (Ceballos and Ehrlich 2002).

Knowledge of historical species ranges is important for work with endangered species, because recovered or recovering species have been found to occupy a greater percentage of their historic range than declining species (Abbitt and Scott 2001). Although conservation biologists often focus on endangered species, the loss of populations should be of equal concern (Ehrlich and Daily 1993, Ceballos and Ehrlich 2002). If range contractions are large, the loss of populations can be considerable, and if range fragmentations occur as well, species may well move to the brink of extinction.

In this study, we did not consider species abundance within the range, although we realize this is an important factor because range contractions often occur in areas of high species abundance (Rodriguez 2002). For conservation strategies, this means that a small decrease in geographical area may result in a considerable loss of animals. Further studies would benefit from including this information, although we recognize that acquiring species abundance data at the scale of North America may be a difficult task. Our study of species range changes and their relationship to human influence was done at a relatively coarse scale. We also acknowledge the shortcomings of the historic and current species range maps, which led us to investigate only those species that had experienced range contractions over more than 20% of their historic range.

Nevertheless, our study shows that species contractions are a major result of Euro-American settlement and post-settlement development in North America. The effects have been widespread and indicate a rapid collapse of species distributions over the course of only a century or two. Unless human impacts and concerns for native species change in the coming years and decades, further range contractions are assured. We envision that our research into human influences on species range changes will be of use to conservation biologists and restoration ecologists developing predictions for further range contractions, designing parks and reserves, assisting in the management of declining species, and providing up-to-date information for wildlife reintroductions.

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