BIOLOGY AND CONSERVATION OF

MARTENS, SABLES, AND FISHERS

A New Synthesis

EDITED BY

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Distribution Changes of American Martens and Fishers in Eastern North America, 1699–2001

WILLIAM B. KROHN

ABSTRACT

Contractions in the geographic distributions of the American marten (*Martes americana*) and fisher (*M. pennanti*) in eastern North America south of the St. Lawrence River between Colonial times (ca. 1650–1800) and the fisher's recent range expansion (ca. 1930–present) are well documented, but causal factors in these range contractions have only partially been studied. Traditional explanations for range contractions by both species are forest clearing and unregulated trapping; little consideration has been given to alternative explanations. It has been hypothesized that deep snow limits the distribution of fishers, and that high fisher populations limit the distribution of martens. I assessed the potential contributions of these factors to observed range contractions for these species by evaluating expected patterns of change in their historical distributions since Colonial times. Using published data on the distribution of martens and fishers in eastern North America, including early and contemporary fur-harvest records ($n = 60{,}702$), I found that broad-scale changes in their geographic distributions in eastern North America were consistent with 3 of those expectations, and partially so with a 4th. I recognize that retrospective analyses cannot establish the relative importance of land clearing, unregulated trapping, and changing climatic conditions on observed range contractions; nevertheless, when historical data from eastern North America are viewed in the context of long-term climate warming and the results of recent ecological studies, they suggest that traditional arguments may only partially explain historical range contractions for both species. This study further suggests that under a warming climate, northern range boundaries for the fisher will expand, and southern range boundaries for the American marten will continue to contract.

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Introduction

Documented contractions in the geographic distributions of many species of North American wildlife since the Colonial era (ca. 1650–1800) are usually attributed to habitat loss or overharvest (i.e., trapping, hunting, or a combination of both), with little consideration given to alternative explanations. For example, it is well documented that compared with the late 1700s through 1800s, the ranges of the American marten (*Martes americana*) and fisher (*M. pennanti*) have decreased substantially in eastern North America (e.g., Seton 1909, 1929; Hagmeier 1956; Gibilisco 1994; Proulx et al. 2004). Despite this extensive documentation, formal investigations of the underlying causes have not been conducted, and biologists continue to attribute these range losses solely to unregulated fur harvests and loss of forested habitats. For example, Strickland and Douglas (1987: 532) wrote that the marten's "most suitable habitat has been lost throughout the southern primordial range as a result of land clearance. . . . In some areas where adequate habitat persisted, overtrapping caused local extirpation." Powell (1994a: 11) stated that "American martens and fishers reached their nadir early in this century owing to overexploitation for fur and to habitat loss," and Whitaker and Hamilton (1998: 439) wrote that "in the late 1800s and early 1900s [the fisher] was extirpated over most of its eastern range by over-trapping and loss of habitat." Although timber harvesting (Black 1950; Ahn et al. 2002) and unregulated trapping (Moloney 1931; Ray 1987) were widespread activities historically that likely affected these 2 species at some locations during some time periods, they may not have been the only factors involved.

There is increasing recognition that relatively recent climatic changes have altered the distributions and abundances of numerous plant and animal species (e.g., Schneider and Root 2002). Krohn et al. (1995, 1997) proposed 2 hypotheses relating to the distribution of martens and fishers that involved climate: (1) deep snow limits the distribution of fishers, but not of martens, as a result of much higher energy costs for fishers to travel or hunt in such conditions (a direct climatic effect); and (2) high fisher populations limit the distribution of martens, possibly because of interference competitions by fishers (primarily predation, an indirect climatic effect).

Generally, species distributions are limited at northern range boundaries by abiotic factors, whereas at southern range boundaries, where environmental conditions tend to be less extreme, they are limited by biotic interactions (Brown and Lomolino 1998). The notion that fishers are limited in the north (and at high elevations) by deep snow, whereas martens are limited in the south (and at low elevations) by competitive interactions with fishers, is consistent with this generality. Moruzzi et al. (2003) assessed an unsuccessful reintroduction of martens in the Green Mountains National Forest of

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southern Vermont and concluded that failure may have been due to competition with fishers. In contrast, there is evidence of a slowly recovering marten population in the highlands of northern New Hampshire (Kelly et al. 2009b), which is an area of considerably deeper and more extensive snowfalls than southern Vermont (Krohn et al. 2004). Carroll (2007) reported correlations across eastern North America in the broad-scale occurrence of American martens with mean annual snowfall >300 cm/year and certain forest types (i.e., mature conifer and mixed). A large genetic study of fishers ($n = 769$) from southeastern Ontario through northwestern New York concluded that snow depth was an important component of fisher habitat; as snow depth increased, the proportion of immigrants in an area also increased (as occurs in sink habitats), suggesting that deep-snow environments were of lower quality (Carr et al. 2007b). In a recent study in northern Idaho, Albrecht et al. (2009) found that fishers were associated with forestlands with low snowfall, whereas martens were generally associated with deep snowfall areas; in addition, martens were recorded in some low-snowfall forests that lacked fishers, suggesting that fishers may limit martens. Fisher predation was the major cause of natural mortality in studies of >100 radio-collared martens in north-central Maine (Hodgman et al. 1997; Payer 1999). These studies occurred in a region of relatively deep snow and few fishers (Maine Dept. of Inland Fisheries and Wildlife, unpublished harvest data). In northern Wisconsin, predation by fishers and raptors was the major natural source of mortality of adult martens (too few juveniles were captured to estimate mortality in this age class) in a population that failed to expand >30 years after being reintroduced (McCann et al. 2010). Although the preceding studies did not demonstrate that fishers limited marten populations, interspecific predation is common among carnivores (Palomares and Caro 1999), especially among similar species, and predation rates increase with differences in body sizes between predator and prey (Donadio and Buskirk 2006). In the East, the average body mass of fishers is 5.4–6.5 times larger than that of martens (Krohn et al. 2004).

In this chapter, I examine historical changes in the geographic distributions of American martens and fishers, both of which were once abundant and widely distributed throughout the forested regions of eastern North America (i.e., south of the St. Lawrence River and east of the Great Lakes). I give special attention to identifying spatiotemporal patterns in historical fur-harvest records for martens and fishers, and determining whether or not observed patterns are consistent with the expectations that follow from the fisher/snow and fisher/marten hypotheses. If historical patterns are consistent with those expectations, they may provide new insights into reasons the distributions of these species have changed substantially during the last 300 years or so.

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Approach, Expectations, and Data

The Little Ice Age (LIA) was a climatically cool period that occurred from ca. 1450 to 1800 (Imbrie and Imbrie 1986). This was also a period of more severe and frequent storms, especially at higher latitudes; in the Northern Hemisphere, the LIA was an exceptionally cold and snowy era (Imbrie and Imbrie 1986; Grove 1988; Mann 2002). In the northeastern United States, the 1600s and 1700s were considerably colder and snowier than they are now (Baron 1992; Zielinski and Keim 2003). Thus, during the LIA, heavier and more persistent snow cover would likely have occurred farther south and at lower elevations in eastern North America than they do currently.

If the fisher/snow and fisher/marten hypotheses are true, then I would expect the historical distributions of martens and fishers to have been much different than they are today, both elevationally and latitudinally. During the Colonial era, which occurred when areas of deep snow presumably reached their maximum extent, I would expect that (1) both species would have occurred farther south than they do now, with fishers occurring farther south than martens; and (2) martens would have had a more continuous distribution than they do now (i.e., less restricted to higher elevations, since deeper snow would have shifted fishers southward). After the LIA ended during the early 1800s, and areas of deep snowfall began contracting in geographic extent, (3) the southern edge of the marten's range would have shifted northward, and martens would have become more restricted to higher elevations. The fisher's northern range boundary would also have shifted northward compared with Colonial times, but fishers would have retained a more southerly distribution than that of martens. Last, given the hypothesized negative effect of dense fisher populations on marten survival, (4) during both time periods, areas supporting high fisher populations would have had low populations of martens, and vice versa.

To obtain data useful for evaluating these expectations, I started with references listed in Seton (1909, 1929) and Hagmeier (1956). Hagmeier's seminal paper on marten and fisher distributions was especially useful because he presents data sources by individual states and provinces, so his references are more spatially explicit than Seton's, which are based on more general sources. Because martens and fishers (along with American beavers [*Castor canadensis*]) were important target species during the early fur trade in North America, 18th- and 19th-century fur records were available for study (Moloney 1931; Ray 1987). Truck (i.e., fur-trade) houses were established in the American colonies during the 17th and 18th centuries, well before the western fur trade developed; although most of these records were lost to fires (especially those archived in Boston), a few have survived. I also examined published reports from natural history surveys conducted during

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the 19th century in all northeastern states (Merrill 1920), along with 19th- and early 20th-century technical and scientific literature on these 2 species in the East. During these time periods, trapping records were located in sporting (i.e., fishing, hunting, trapping, natural history) books and journals. For example, *Forest and Stream*, a popular outdoor sporting journal during the 1800s and early 1900s, regularly contained articles by prominent scientists and amateur naturalists of the day, as well as some written by trappers.

Previous studies of historical occurrence records have been largely descriptive; in contrast, I gave special attention to locating and evaluating documented fur-harvest records. When studying historical changes in species distributions, written records have 2 major advantages over descriptive accounts: they represent quantitative counts that can be analyzed, and they are less subject to misidentification because the observer had the opportunity to handle and study the animals. Furthermore, because martens and fishers were common in the eastern fur trade, both historically and recently, they are less subject to observational error than are rare or elusive species (see McKelvey et al. 2008). Clearly, however, the reliability of such records is only as good as that of the people who recorded them. Consequently, I used information from nonprofessional observers (e.g., trappers) only when I believed those persons to be reliable sources (see biographical sketches in Krohn and Hoving 2010: 475–506).

There is a strong latitudinal gradient of declining mean annual snowfall from north to south in eastern North America (e.g., Zielinski and Keim 2003: 86; Krohn et al. 2004: 125). To evaluate relative changes in the distributions of these 2 species over time along this spatial gradient, I tabulated fur-harvest records for various time periods to determine whether the ratio of martens to fishers in the harvest was highest in the north (region with greatest snowfall), and lowest in the south (region with little or no snowfall where fishers predominated). Similarly, when assessing changes in marten-to-fisher ratios in a given area over time, I expected a decrease in the ratio of martens to fishers in the fur-harvest as that area warmed near the end of the LIA, and environmental conditions presumably improved for fishers.

By their nature, historical data are incomplete and must be interpreted cautiously. For example, in 1546, the French were trading with native Americans at the mouth of Chesapeake Bay for "as many as a thousand marten skins" (Quinn 1979: 218). While such an early observation is interesting, I did not include it in this analysis. During the initial days of European trade in eastern North America, extensive native trade routes were still intact. For example, skins of the American bison (*Bos bison*) were transported from the Appalachian and Allegheny mountains down major eastern rivers and northward along the coast, where they were traded with natives in eastern Canada. Bison skins were highly prized as flooring in winter quarters. Once Native

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Americans formed alliances with the competing European powers, however, trade quickly became more local. For example, with the French and English competing west of the Appalachians, it is highly unlikely that any quantities of northern furs controlled by the French would be traded in Virginia (Crane 1928; Parrish 1972).

Results

Expectation 1: Southern Boundaries for American Martens and Fishers

Ernest Thompson Seton published the earliest detailed range maps for martens (Seton 1909: 905; 1929: 485) and fishers (Seton 1909: 929; 1929: 455), showing that both species occurred much farther south historically than they do today (Figure 4.1). The sources for Seton's range limits are given in the legend of his maps, although it is not clear exactly what occurrence records he used. A later and more thoroughly documented study was that of Hagmeier (1956), who used about 250 references to delineate historical and current ranges for both species; about 80 of these references reported information from eastern North America. Both Hagmeier (1956) and Seton (1909, 1929) reported that, historically, the southern range limit for the marten was north of that for the fisher. Allen (1876), Coues (1877), and Keay (1901) all described martens and fishers as common inhabitants of forests south of New England. The southern range limits for both species were reported to occur farther south during the 1800s than they do now; Audubon and Bachman (1852) recorded fishers as far south as the mountains of North Carolina and Tennessee, and Rhoads (1903) reported that martens occurred as far south as north-central Pennsylvania during the early 1800s.

Fur-harvest records from the British Colonial Office document the number of pelts exported from Virginia to England from 1699 to 1715 (Table 4.1). Both species were regularly shipped in large numbers during this 17-year period, with reported totals of 1432 martens and 3355 fishers (Table 4.1). Interestingly, the wolverine (*Gulo gulo*), which like the marten is associated with deep snow (Aubry et al. 2007), was exported in low numbers in 1699 and 1704 (Table 4.1).

In summary, records from early explorers, fur traders, and naturalists showed that fishers ranged as far south as the Cumberland Plateau from the late 1600s to the early 1800s. Martens occurred north of fishers (Seton 1909, 1929; Hagmeier 1956), and continued to occur as far south as north-central Pennsylvania into the late 1880s (Rhoads 1903). Thus, consistent with Expectation 1, both species were reported to occur farther south in historical times than they do now, and fishers occurred farther south than martens.

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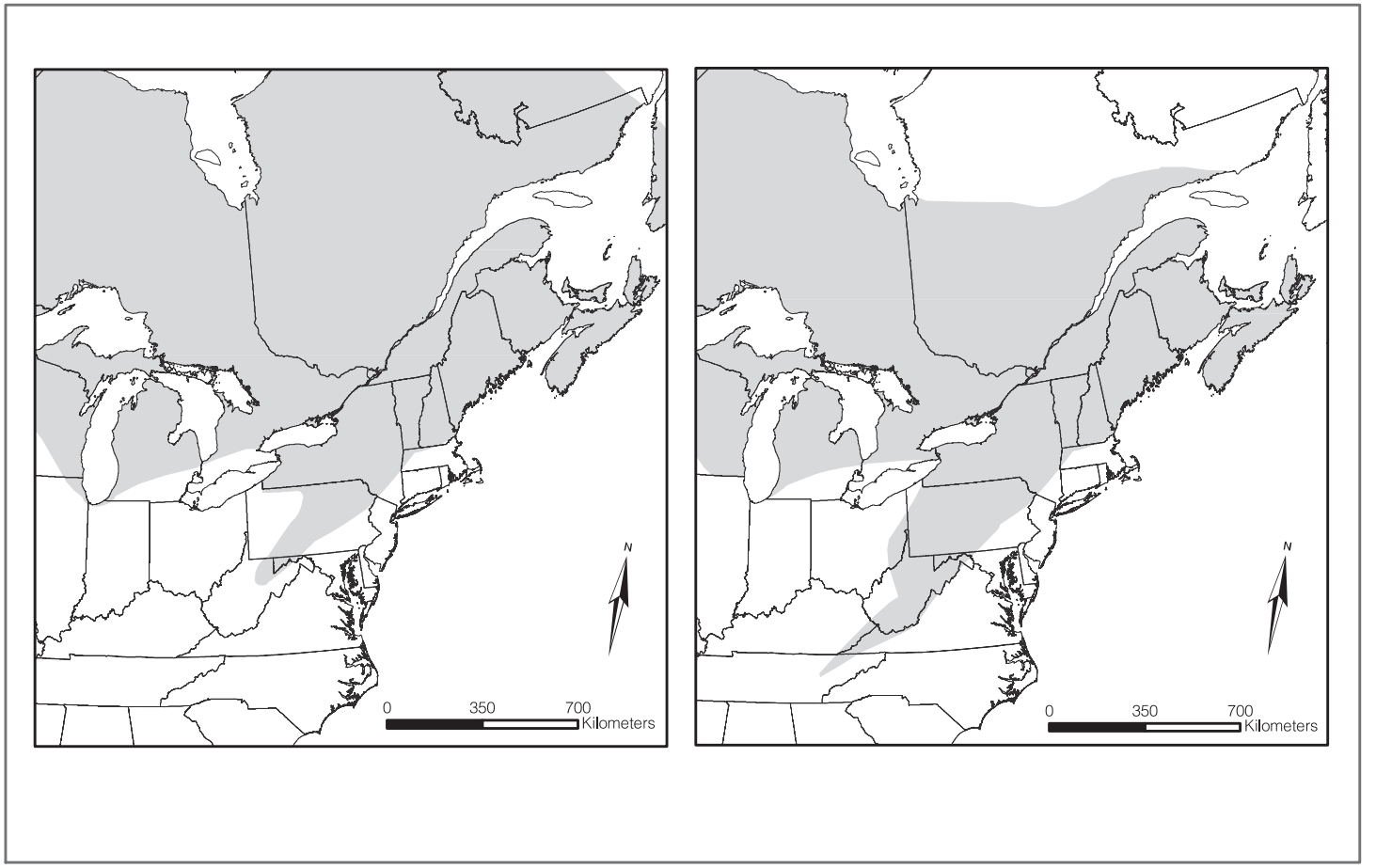

Figure 4.1. Historical distributions of the American marten (*left*) and fisher (*right*) in eastern North America (Seton 1909: 905, 929). Hagmeier's (1956) range maps indicated that the southernmost distribution of fishers included the mountains of western North Carolina and eastern Tennessee, and that American martens occurred along the coast in southern New England.

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Table 4.1. Number of American marten, fisher, and wolverine pelts exported from Virginia to England from 1699 to 1715

Year	American marten	Fisher	Wolverine[a]
1699	5	163	7
1700	0	106	0
1701	0	70	0
1702	0	463	0
1703	0	5	0
1704	58	58	4
1705	112	108	0
1706	4	97	0
1707	0	0	0
1708	0	416	0
1709	12	496	0
1710	35	18	0
1711	76	1100	0
1712	1130	151	0
1713	0	0	0
1714	0	90	0
1715	0	14	0
Total	1432	3355	11
Mean	84	197	0.65

Sources: British Colonial Office (CO) Papers (Microfilm: CO class 5, reel 10, frames 133–135); Hagmeier (1956: 162, 164) labeled these data the "Account Showing the Quantity of Skins and Furs Exported Annually . . . from Virginia from . . . 1698 to . . . 1715." His source of this information was "Bailey, J.W. 1946. The Mammals of Virginia . . . Richmond, privately printed, 416 p."

Note: Harvest data were also reported for beaver, deer, moose (*Alces alces*), and other wildlife species (not shown here)

[a] The broad-scale occurrence of the wolverine, like American marten (Carroll 2007) and Canada lynx (Hoving et al. 2005), is strongly associated with deep snows (Aubry et al. 2007). Thus, with historical climate warming in eastern North America, the ranges of all 3 species would be expected to have declined, as has been documented (marten, this study; lynx, Hoving et al. [2003]; wolverine, Krohn and Hoving [2010]).

Expectation 2: Distribution of American Martens—Continuous or Disjunct?

Both species occurred throughout the interior forests of eastern Canada (Hardy 1869; Adams 1873), through New England (Emmons 1840; Thompson 1842; Allen 1876) and New York (DeKay 1842; Merriam 1882), and into north-central Pennsylvania (Rhoads 1903). Keay (1901) reviewed 15 early accounts published between 1524 and 1675, and considered both species to be common and distributed continuously throughout New England during the Colonial era, except along the coast. Allen (1876: 713–714) reported that both martens and fishers "were common inhabitants of not only the whole of New England, but also of the Atlantic States generally as far south as Virginia

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(excepting possibly a narrow belt along the seaboard)." Fur-harvest records compiled for this study also show that, during historical times, martens and fishers were reported to be more widely distributed than they are today. Thus, consistent with Expectation 2, martens were reported to occur continuously from the interior forests of Pennsylvania north through New York and New England into eastern Canada (e.g., Keay 1901; Rhoads 1903). Although martens did not occur in coastal forests, I found no indication in the historical record that they were limited to interior highlands and mountains.

Expectation 3: Northward Range Shifts after the Little Ice Age

In the 9 states where martens occurred historically, the species was extirpated in all but Maine and New York (Table 4.2); and, in the 15 states where fishers occurred historically, the species was apparently extirpated in all but Maine, Vermont, New Hampshire, and New York (Table 4.2). In New York, both species persisted only in the Adirondack Mountains in the east-central part of the state. In the states that supported both species historically, and where the year of extirpation had been reported, martens tended to be extirpated before fishers (Table 4.2), suggesting that the 2 species were not equally vulnerable to the factors causing extirpation. If deep snow was the main factor reducing contact between martens and fishers, then as the climate moder-

Table 4.2. Approximate years in which American martens and fishers were extirpated in the eastern United States during the 19th and 20th centuries

State	American marten	Fisher
Maine	never extirpated	never extirpated
Vermont	1926	almost extirpated[a]
New Hampshire	1940	almost extirpated[a]
Massachusetts	historically present[b]	~1900
Connecticut	historically present[b]	after 1924
Rhode Island	no record of occurrence	~1938
New York[c]	1930	almost extirpated
Pennsylvania	1900	1903
New Jersey	1853	~1889
Maryland	1880	probably present historically
West Virginia	no record of occurrence	rare in 1911
Virginia	before 1851	1890
North Carolina	probably absent	1854
South Carolina	probably absent	probably present historically
Tennessee	probably absent	1881

Source: Hagmeier (1956) unless otherwise footnoted
[a] Nearly went extinct during the 1920s and 1930s (Hagmeier 1956; Silver 1957)
[b] In the mountains in the western part of the state
[c] Excluding the Adirondack Region, where both species survived at higher elevations (DeKay 1842; Merriam 1882)

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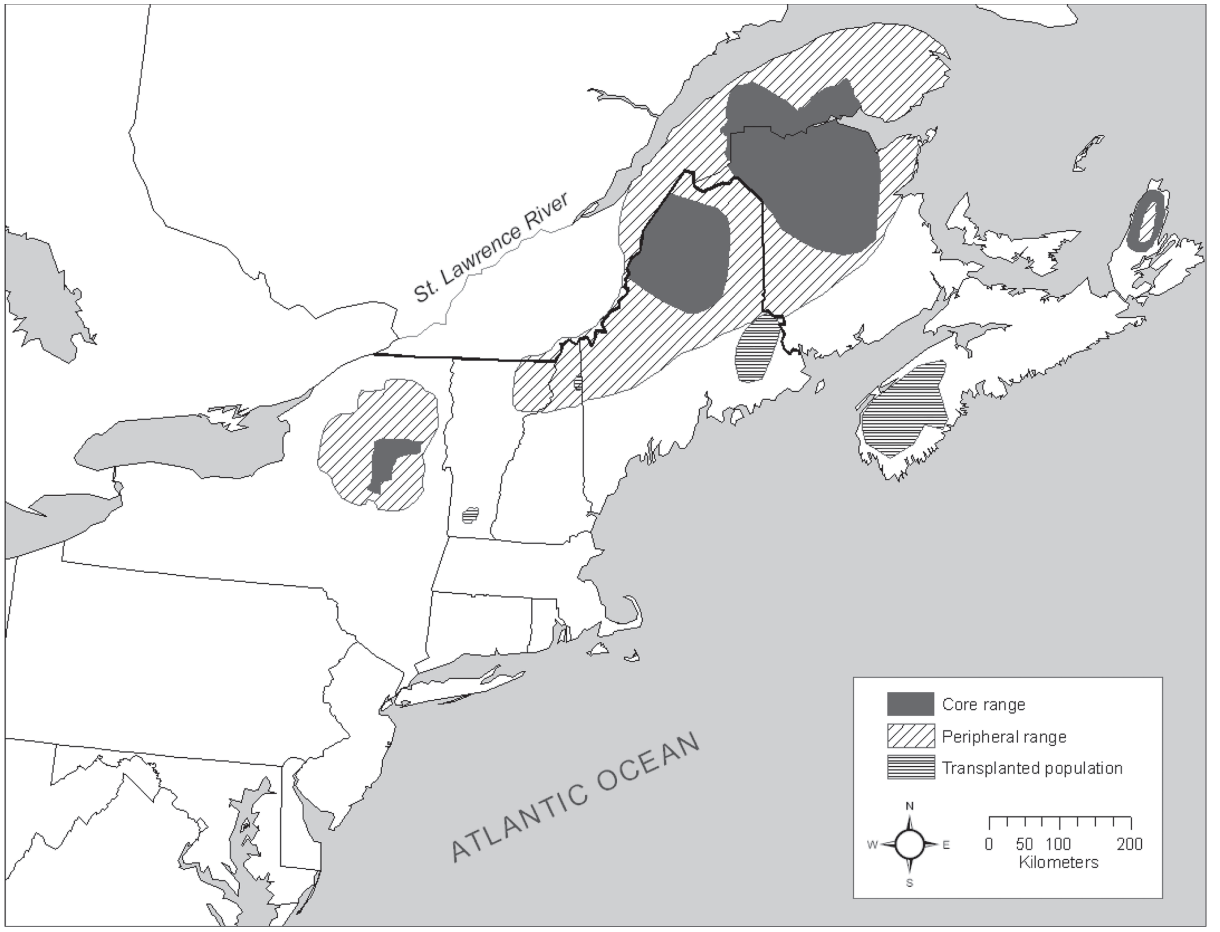

Figure 4.2. Current range of the American marten in eastern North America south of the St. Lawrence River, based on harvest densities (Krohn et al. 1995; Carroll 2005b) and information provided by furbearer biologists in these states and provinces. Note that the highlands of Cape Breton Island and the northeastern Gaspe Peninsula are both high-elevation, deep-snowfall areas, but are not part of the marten's core range, apparently because both are essentially unforested as a result of extreme environmental conditions. The current status of transplanted marten populations is variable, but they do not appear to be robust, high-density populations (e.g., Moruzzi et al. 2003; Kelly et al. 2009b).

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ated, marten populations should have contracted northward and to higher elevations, whereas fisher populations should have expanded into areas where snowfall deceased substantially. The current distribution of martens is consistent with this hypothesis; they are no longer distributed continuously in interior forests and have become restricted to relatively high-elevation areas at higher latitudes (Figure 4.2). However, both martens and fishers were extirpated in many eastern states (Table 4.2). Fishers did not persist as expected; rather, their range contracted along with that of martens, although this was not as extensive geographically. Because all my findings were not consistent with Expectation 3, this suggests that climate change was not the only factor causing range contractions in these 2 *Martes* species after the end of the LIA.

Expectation 4: Relative Abundance of American Martens and Fishers

To examine changes in the relative abundance of both species across time and space, I evaluated 12,250 historical and 48,452 contemporary fur-harvest records. The ratio of martens to fishers reported from fur-harvests in Virginia from 1699 to 1715 was 0.43:1 (n = 4787) (Table 4.1) compared with 24.8:1 (n = 6821) for fur records from Machias, Maine (near the New Brunswick border) and St. John (Pleasant Point), New Brunswick from 1764 to 1778 (Table 4.3). The ratio of martens to fishers documented by trappers in Maine and New Brunswick from 1850 to the early 1900s was 8.58:1 (n = 642; Table 4.4). Thus, historical and recent fur-harvest records indicate a steady decrease in the ratios of martens to fishers in Maine and New Brunswick during the last 250 years (Tables 4.4 and 4.5). Although the number of fishers harvested increased relative to martens in both areas, the marten-to-fisher ratio was higher in New Brunswick than in Maine during the latter 2 time periods (1850–early 1900s and 1997–2001; Table 4.5).

Altogether, the ratios of martens to fishers in fur-harvest records was 58 times greater (= 24.8/0.43; n = 11,608) in the northern part of their range (i.e.,

Table 4.3. Number of American martens and fishers reported harvested from Maine and New Brunswick from 1764 to 1778

Location	Time period	American martens	Fishers	Source
Machias, Maine, USA[a]	1777–1778	367	6	Anonymous (1779)
Portland Point (St. John), New Brunswick, Canada	1764–1775	6190	258	Raymond (1950: 157–158)[b]

[a] Located 42.6 km southwest of the border with New Brunswick, Canada
[b] Numerous other furbearer pelts shipped, including 8 wolverine and 67 Canada lynx

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Table 4.4. Documented harvests of 3 furbearers during fur hunts in the mid-1880s to early 1900s in northern Maine, USA and New Brunswick, Canada

Year(s)	Location	Species harvested			Source
		American marten	Fisher	Lynx[a]	
1850	Restigouch and Kedgwick rivers, New Brunswick	108	0	2	Palmer (1949: 3–4)
1858	Northern Maine and upper Tobique and Nepsiquit rivers, New Brunswick	19	1	2	Journal and Letter[b]
1859	Caucogomoc Lake region, northern Maine	~50	4	3	Hardy (1910: 929)
1860	Northwest of Chensuncook Lake, northern Maine	0	2	15	Palmer (1949: 13)
1860–61	Northwest of Chensuncook Lake, northern Maine	100	9	20	Hardy (1903: 263)
1862	Tobique River country, New Brunswick	9	9	10	Palmer (1949: fn 37)
1865	Patten area of north-central Maine	1	1	3	Letter[c]
1868	Patten area of north-central Maine	1	8	3	Letter[d]
1876–77	Upper Magalloway River and Parnachenee Lake, western Maine	49	15	6	Barker and Danforth (1882: 238)
1891–92	North-central New Brunswick	98	0	22	Braithwaite (1892: 6)
1894–95	Rangeley Lakes region of western Maine	30	7	0	Anonymous (1895: 6)
1895–96	Upper Magalloway River and Parmachenee Lake, western Maine	50	4	0	Haywood (1897: 107)
early 1900s	Gulquac River (tributary of the Tobique River), New Brunswick	60	7	0[e]	Shaw (1987: 48)
Totals		575	67	86	

[a] See footnote a in Table 4.1

[b] Journal by Manly Hardy titled "Notes of a Trip to Tobique—1858," and a letter from William H. Staples to Manly Hardy dated February 3, 1859 (both are located in the Manly Hardy Collection [MHC], Special Collections, Raymond H. Fogler Library, University of Maine, Orono), or see Krohn (2005)

[c] Letter from William H. Staples to Manly Hardy dated December 16, 1865 (MHC)

[d] Letter from William H. Staples to Manly Hardy dated April 28, 1868 (MHC)

[e] By 1900, bobcats had moved inland and outnumbered lynx throughout northern New England and eastern Canada (Hoving et al. 2003)

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Table 4.5. Temporal changes in the ratio of American martens to fishers in fur harvests from Maine and New Brunswick, 1764–2001

Period (source)	Maine (*n*)	New Brunswick (*n*)
1764–1778 (Table 4.3)	Data pooled with New Brunswick[a]	24.8 (6821)
1850–early 1900s (Table 4.4)	5.9 (351)	17.2 (291)
1997–2001 (harvest records)[b]	1.6 (32,000)	3.6 (16,452)

[a] The Maine sample was obtained near the Maine/New Brunswick border; thus, for this time period, samples from Maine (n = 373) and New Brunswick (n = 6448) were pooled

[b] Maine data courtesy of the Maine Department of Inland Fisheries and Wildlife; New Brunswick data courtesy of the New Brunswick Fish and Wildlife Branch

Maine and New Brunswick) than in the southern part (i.e., furs exported from Virginia) from 1699 to 1778. Also, marten-to-fisher ratios were higher in New Brunswick than in Maine. Thus, as climatic conditions warmed and snowpacks decreased, the ratios decreased steadily through time in both areas from 1764 to 2001 (n = 55,915).

Discussion

This was a retrospective assessment, preventing me from evaluating relevant factors independent of potentially confounding conditions. Thus, I cannot rule out overtrapping or forest clearing as important factors contributing to range losses for both *Martes* species in the East. Furthermore, because the fisher failed to expand or even maintain its range when climatic conditions warmed after the LIA, factors other than climate change clearly played a role. The northward pattern of range contraction, however, and the fact that martens apparently responded before fishers, are consistent with climatic warming as a causal factor but inconsistent with historical patterns of European settlement, forest clearing, and agricultural development. Although deforestation occurred throughout the eastern United States (it was much less extensive in eastern Canada) and, in some states, resulted in more cleared than forested land (e.g., Black 1950; Ahn et al. 2002), deforestation did not occur in a south-to-north pattern, nor was it uniform throughout the East (Greeley 1925). Colonial land clearing and settlement occurred westward from the initial European settlements centered in a core area from Boston to Philadelphia (Walker 1872; Greeley 1925), suggesting a pattern that would have split marten and fisher populations into separate northern and southern areas. In 1850, the Appalachian Mountains south of New York State were still covered with virgin forests (Greeley 1925). Even as late as 1920, numerous large areas (>25,000 acres) of virgin forests still remained in the Appalachians south of Pennsylvania (Greeley 1925). Thus, it appears that these forests were still structurally capable of supporting martens and fishers, yet the southern Appalachians experienced the earliest extirpations of both species (Table 4.2).

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The fur trade was a major economic activity of the early settlers and occurred throughout eastern North America. Although the fur trade targeted different species in various regions (e.g., white-tailed deer [*Odocoileus virginianus*] in the south and beaver in the north), the geographic expansion of fur harvesting occurred along numerous fronts and was not unidirectional across eastern North America (Crane 1928; Moloney 1931; Parrish 1972; Ray 1987). Thus, the extirpation of martens and fishers by overtrapping would not be expected to proceed from south to north, but such a pattern would occur if climatic warming were a major causal factor in observed range dynamics.

In this study, I have provided evidence that the geographic distributions of the American marten and fisher contracted in eastern North America after the close of the LIA, and that the relative abundance of these 2 species varied in both time and space. If the contraction of southern range boundaries for these 2 species were due simply to forest clearing and unregulated trapping, then both species should have reoccupied their former ranges when these limiting factors were removed. Since Colonial times, eastern forests have recovered (e.g., Black 1950; Ahn et al. 2002), and fur harvests are now regulated by states and provinces (Proulx et al. 2004). The fisher has been expanding its range recently but does not occur as far south as it did historically, whereas marten populations are stable or decreasing (Gibilisco 1994; Proulx et al. 2004). Fishers occur from eastern Canada south through New York State, and populations are increasing throughout southern New England. In addition, reintroduced populations are expanding their distribution throughout Connecticut, southern New York, Pennsylvania, and the highlands of West Virginia (Proulx et al. 2004). In contrast, marten reintroductions have been less successful (e.g., Moruzzi et al. 2003). Not only has the range of the marten failed to increase since the end of the LIA, but populations in northeastern North America also appear to be becoming more insular and disjunct (Figure 4.2). This increased geographic isolation of the marten in the East is occurring despite carefully regulated trapping and extensive forest cover across the region (see satellite map in Google Earth). More recently, however, forest practices in Maine have reduced marten habitat independent of climate change (Simons 2009).

In coastal Maine and southern New England, mean annual temperatures increased by >1 °F (0.6 °C) from 1895 to 2000, whereas in northern Maine they decreased by >1 °F (Zielinski and Keim 2003: 249–250). Northwestern Maine receives greater snowfall than the coastal and southern portions of the state (Zielinski and Keim 2003: 83–88). High snowfall is a consistent feature of the areas in eastern North America that still support core marten populations (i.e., the areas with abundant marten populations based on consistently high harvest records; Carroll 2007). These currently include Cape Breton Island in Nova Scotia, north-central New Brunswick and adjacent forested

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areas on Quebec's Gaspe Peninsula, northwestern Maine, and the Adirondack Mountains in New York State (Figure 4.2).

In the Hudson Bay region of Canada, Preble (1902: 68–69) reported that fishers were "found sparingly throughout the southern part of the region" whereas "the marten is fairly common throughout the region north to the tree limit." If the range of fishers is strongly tied to low snowfall levels, then I would expect fisher populations to expand their northern range boundary when climatic conditions become warmer. Interestingly, the ratio of martens to fishers in the harvest records of the Hudson Bay Company decreased from 83.9:1 in 1739–1748 (n = 146,086) to 65.9:1 in 1790–1799 (n = 197,180), 16.8:1 in 1840–1849 (n = 900,032), and 18.7:1 in 1890–1899 (n = 864,689) (Novak et al. 1987: 71–72, 115–116). Harper (1961: 114) noted that fishers occur farther north in western than in eastern Canada (i.e., the Ungava Peninsula), and suggested that the greater mean annual snowfall in the Ungava Peninsula compared with western Canada (330–508 vs. 102–154 cm) might restrict fisher movements and hunting success. Moreover, Brown and Braaten (1998) documented a decrease in snowfall throughout Canada during the past 40–50 years, suggesting the need for a formal assessment of broad-scale changes in marten and fisher populations in relation to snowfall dynamics and other factors (e.g., harvest pressure) in Canada.

Evaluation of Expectation 4 was based on ratios in trapping data, which could be biased if trapping vulnerability varied among areas or changed over time. Although juveniles of both species are more vulnerable to trapping than are adults (Krohn et al. 1994; Hodgman et al. 1997), I found no evidence that suggested the presence of any spatial or temporal biases in the historical data. Although modern trappers commonly use metal body-gripping traps to catch both species, in earlier times deadfalls were widely used for both species (e.g., Adney 1893a,b; Seton 1909: 921). Thus, while the materials used to harvest these 2 species has changed over time (i.e., wood vs. steel), the basic concepts underlying these traps are remarkably similar (i.e., to quickly suffocate the animal). Marten-to-fisher ratios would also be biased if trappers or fur dealers reported captures of 1 species more frequently than the other; however, I had no reason to suspect differential reporting, because both species were highly prized in the fur trade and were commonly trapped, traded, and shipped (Novak et al. 1987; this study).

This study hinges on the assumptions that snowfalls during the Colonial era were heavier and more extensive than they are today, and that snowfall has decreased steadily from south to north since the close of the LIA. Because the period covered by this study predates the widespread measurement and recording of weather data, including snowfall patterns, it is not possible to evaluate the validity of these assumptions. Nonetheless, there is considerable anecdotal evidence suggesting that past climates were colder and snowfall was greater (see Jacobson et al. 2009 for a compilation of studies in northern

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New England). In general, the climate in New England has warmed over the last 100 years, whereas the mean annual temperature in northwestern Maine, which still supports viable populations of both American martens and Canada lynx (2 species known to have broad-scale associations with deep-snowfall environments), decreased by 0.4 °F (0.2 °C) from 1895 to 2000 (Zielinski and Keim 2003: 249–250).

Historical data provide a potentially rich and largely untapped source of information for documenting long-term distributional changes in wildlife populations. They may also provide opportunities to evaluate contemporary species-habitat relationship models when such models include a climatic variable as a significant determinant of species occurrence (e.g., snowfall for the marten, lynx, and wolverine). Although historical data have limitations and can be problematic (Edmonds 2001; Sagarin 2002; Krohn and Hoving 2010), this study shows that they can be useful for studying ecological questions related to large-scale distributional changes. Furthermore, my findings suggest that under a warming climate, the fisher will likely expand its range northward, whereas the American marten will continue to retreat from southern regions (see also Lawler et al. 2009, this volume).

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