BIOLOGY AND CONSERVATION OF

MARTENS, SABLES, AND FISHERS

A New Synthesis

EDITED BY

Keith B. Aubry, William J. Zielinski,
Martin G. Raphael, Gilbert Proulx,
and Steven W. Buskirk

First published 2012 by Cornell University Press

Printed in the United States of America

Library of Congress Cataloging-in-Publication Data

Biology and conservation of martens, sables, and fishers : a new synthesis / edited by Keith B. Aubry … [et al.].
p. cm.
Includes bibliographical references and index.
ISBN 978-0-8014-5088-4 (cloth : alk. paper)
1. Martes. 2. Martes—Ecology. 3. Wildlife conservation. I. Aubry, Keith Baker.
QL737.C25B516 2012
599.76'65—dc23 2012003137

Cornell University Press strives to use environmentally responsible suppliers and materials to the fullest extent possible in the publishing of its books. Such materials include vegetable-based, low-VOC inks and acid-free papers that are recycled, totally chlorine-free, or partly composed of nonwood fibers. For further information, visit our website at www.cornellpress.cornell.edu.

Cloth printing 10 9 8 7 6 5 4 3 2 1

20

A Century of Change in Research and Management on the Genus *Martes*

GILBERT PROULX AND MARGARIDA SANTOS-REIS

ABSTRACT

During the 20th century, *Martes* taxonomy, evolution, biogeography, habitat, and populations were investigated extensively, and conservation practices were developed. During this period, human populations and lifestyles, socioeconomics, and cultural and ethical values changed, with a gradual shift away from traditional wildlife uses to nonconsumptive values. In this chapter, we assess trends in research and management practices from 1901 to 2010 in relation to the worldwide conservation of *Martes* species. Based on our review of 1298 publications, we identified 3 distinct time periods in the history of *Martes* research and management: (1) 1901–1960, a utilitarian period when research was focused on species status and distribution; (2) 1961–1990, a period of scientific interest in population declines and habitat deterioration; and (3) 1991–2010, a period of conservation concern for populations and habitats. We review the characteristics of each time period and show that in 110 years of research, wildlife managers and researchers have acquired extensive knowledge about the evolution, taxonomy, morphophysiology, genetics, population dynamics, habitat and predator-prey relations, nutrition and energetics, parasites, and diseases of most *Martes* species. We believe that *Martes* conservation would benefit from better integration of this knowledge into wildlife management programs. The future of *Martes* research and conservation may ultimately depend on integrating the needs of *Martes* species into multispecies management programs, testing whether habitat-management recommendations improve the fitness of target populations, and developing effective education programs.

Introduction

For centuries, the American marten (*Martes americana*), European pine marten (*M. martes*), stone marten (*M. foina*), sable (*M. zibellina*), and fisher

(*M. pennanti*) were renowned for the quality of their pelts, which have been both an article of trade and a currency (Innis 1956; Delort 1986). In the 1900s, when the scientific world became interested in this genus, *Martes* species were still widely distributed throughout Europe, Eurasia, and North America (Delort 1986). During the 20th century, *Martes* taxonomy, evolution, biogeography, habitat, and populations were investigated extensively, and conservation practices were developed. Human populations and lifestyles, socioeconomics, and cultural and ethical values also changed dramatically (Aramburu and King-Dagen 1995; Salwasser 1995). There has been a gradual shift from traditional wildlife uses to nonconsumptive values (Proulx and Barrett 1989; Heberlein 1991; Peterson and Manfredo 1993), as a result of increasing affluence, education, and urbanization (Manfredo et al. 2003).

In this chapter, we assess trends in research and management practices pertaining to the conservation and management of *Martes* species. This assessment includes a review of the ways in which societal changes have affected research themes, and our view of the continuing influence of traditional uses on conservation programs for *Martes* species today.

Methods

We reviewed an extensive body of literature where we expected most *Martes* research to have been published, including key reviews, syntheses, and compendia, such as Powell (1981), Clark et al. (1987), Buskirk et al. (1994), Proulx et al. (1997), Harrison et al. (2004), and Santos-Reis et al. (2006). We also searched all periodicals available digitally through the University of Alberta libraries, and reviewed the content of 13 technical journals: *Zoological Society of London* (since 1830), *Journal of Zoology, London* (since 1832), *Canadian Field-Naturalist* (since 1869), *American Midland Naturalist* (since 1909), *Journal of Mammalogy* (since 1919), *Journal of Animal Ecology* (since 1932), *Journal of Wildlife Management* (since 1937), *Acta Theriologica* (since 1954), *Canadian Journal of Zoology* (since 1929), *Canadian Journal of Forest Research* (since 1971), *Environmental Reviews* (since 1993), *Mammal Review* (since 1970), and *Wildlife Society Bulletin* (since 1973).

We compiled the following information for each article: date of publication, *Martes* species studied, and subject studied; we limited potential study subjects to the following:

1. Populations, with 3 themes: (a) status and distribution, (b) biology, and (c) management
2. Habitats, with 3 themes: (a) home range, habitat use and selection, and landscape characteristics, (b) food habits (food is a resource related to habitat selection, e.g., Baltrūnaitė 2006a), and (c) management programs and models

3. Taxonomy and genetics
4. Other subjects, including studies of morphology, physiology, behavior (e.g., diel activity, curiosity, scent marking), parasites, diseases, economics, and paleontology

A publication could be coded as covering 1 subject (i.e., 1 dataset corresponded to 1 subject) or >1 subject. We considered 2 groups of species based on geography, similar histories of exploitation, and habitat-conservation policies (Proulx et al. 2004): Group (1) the American marten and fisher; and Group (2) the European pine marten, stone marten, and sable. The yellow-throated (*M. flavigula*), Japanese (*M. melampus*), and Nilgiri (*M. gwatkinsii*) martens were excluded because of the paucity of publications on these species. The majority of *Martes* papers were published after 1900. We therefore focused our review on the 110-year period from 1901 to 2010. To obtain adequate sample sizes for statistical analyses, we grouped study subjects into 4 time periods of similar length: 1901–1930, 1931–1960, 1961–1990, and 1991–2010. We knew that interest in *Martes* biology and conservation had increased in the 1990s after the first International *Martes* Symposium was convened in 1991 (Buskirk et al. 1994) and the *Martes* Working Group was created in 1993, so we subdivided the first 90 years of *Martes* publications into three 30-year periods, and used a 20-year period after 1990. We used the proportion of 110 years represented by each period to determine the expected frequency of studies for each period, assuming the null hypothesis of no change in *Martes* publication activity over time. We used Chi-square statistics with Yates' correction to compare observed to expected frequencies of studies among periods (Zar 1999). When >20% of a period had an expected frequency <5, or when any expected frequency was <1, we combined consecutive periods (Cochran 1954). When Chi-square values indicated significant differences, we compared observed to expected frequencies for each period using the G test for correlated proportions (Sokal and Rohlf 1981). We considered P values ≤0.05 to be statistically significant.

Results

We located a total of 1319 *Martes* publications from 1758 to 2010, with 1298 of these published from 1901 to 2010, representing studies of 1402 different subjects. The largest numbers of publications and subjects studied were for American martens and fishers (Figure 20.1).

Taxonomy and Genetics

For the entire analysis period (1901–2010), observed frequencies of taxonomic and genetic studies for *Martes* Groups 1 and 2 differed significantly ($\chi^2 \geq 64.52$, df ≥ 1, $P < 0.001$) from expectation (Figure 20.2). Studies were

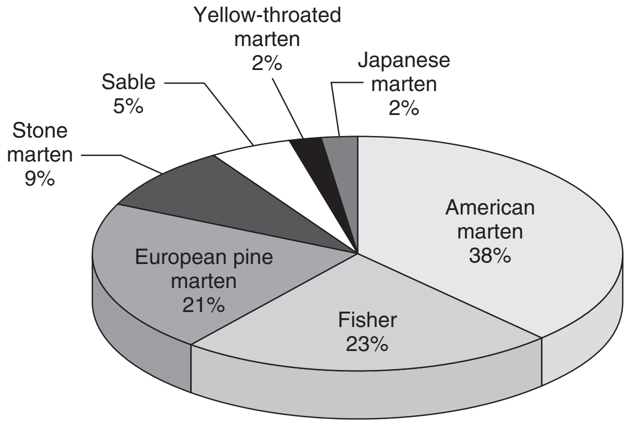

Figure 20.1. Frequency (%) of publications ($n = 1298$) collated in this study for each *Martes* species.

significantly less frequent than expected from 1931 to 1990 for Group 1, and from 1901 to 1990 for Group 2. Studies were more frequent than expected from 1991 to 2010 for both groups (Figure 20.2).

Population

For the entire analysis period, observed frequencies of population studies for *Martes* Groups 1 and 2 differed significantly ($\chi^2 \geq 114.58$, df ≥ 2, $P < 0.001$) from expectation (Figure 20.2). For Group 1, population studies were significantly less frequent than expected from 1901 to 1930, but more frequent than expected from 1991 to 2010 (Figure 20.2). From 1901 to 1960, population studies consisted mostly of status and distribution reports (Figure 20.3). Studies on population biology and management began from 1931 to 1960, but became more important after 1960 (Figure 20.3). In Group 2, studies were significantly less frequent than expected from 1901 to 1960, but more frequent than expected from 1961 to 1990 and 1991 to 2010 (Figure 20.2). Studies on the distribution and biology of species became more important after 1960, and population management programs, after 1990 (Figure 20.3).

Habitat

For the entire analysis period, observed frequencies of habitat studies of *Martes* Groups 1 and 2 differed significantly ($\chi^2 \geq 244.65$, df $= 2$, $P < 0.001$) from expectation (Figure 20.2). Studies were significantly less frequent than expected from 1901 to 1960, but more frequent than expected from 1991 to 2010 (Figure 20.2). Studies on the characteristics of habitats and landscapes increased gradually from 1931 to 2010, and habitat-management programs and models were more frequent from 1991 to 2010 (Figure 20.4).

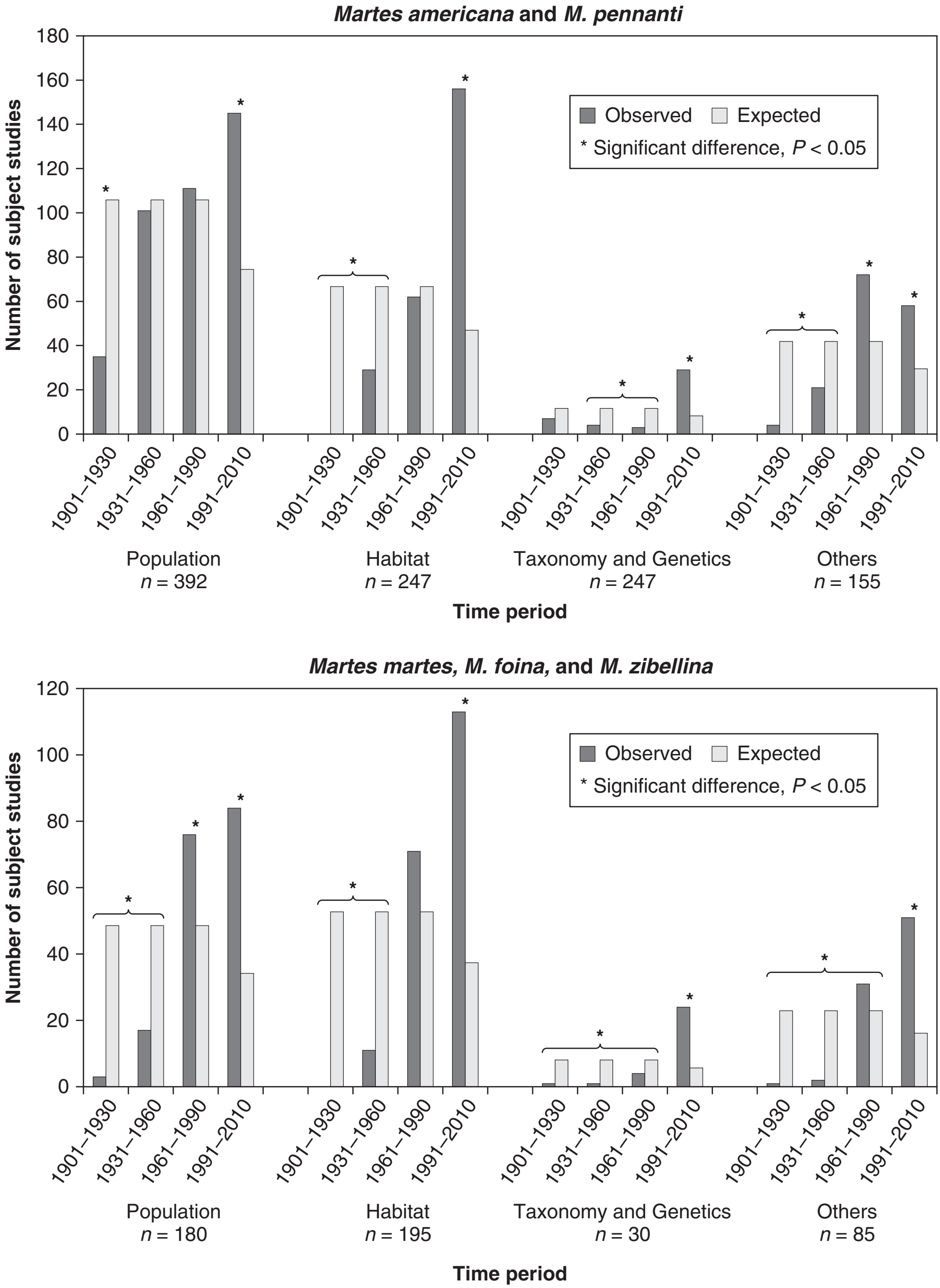

Figure 20.2. Frequency of studies by subject and time period for *Martes* species (brace brackets indicate periods that were pooled for statistical analysis).

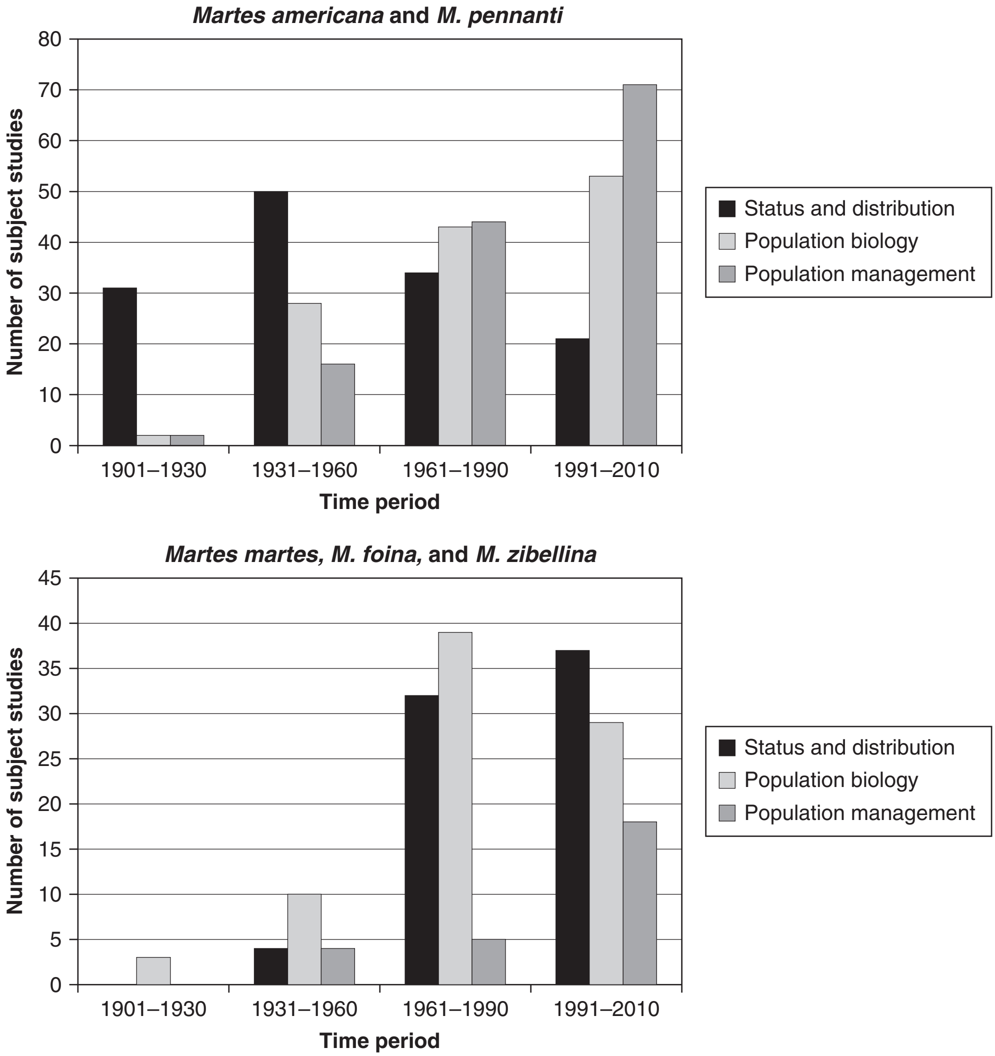

Figure 20.3. Frequency of subtopics for population studies by time period for *Martes* species.

Other Subjects

For the entire analysis period, observed frequencies of other studies for *Martes* Groups 1 and 2 differed significantly ($\chi^2 \geq 68.85$, df ≥ 1, $P < 0.001$) from expectation (Figure 20.2). Studies were significantly less frequent than expected from 1901 to 1960 and 1901 to 1990 for Groups 1 and 2, respectively (Figure 20.2). The frequency of studies was significantly higher than

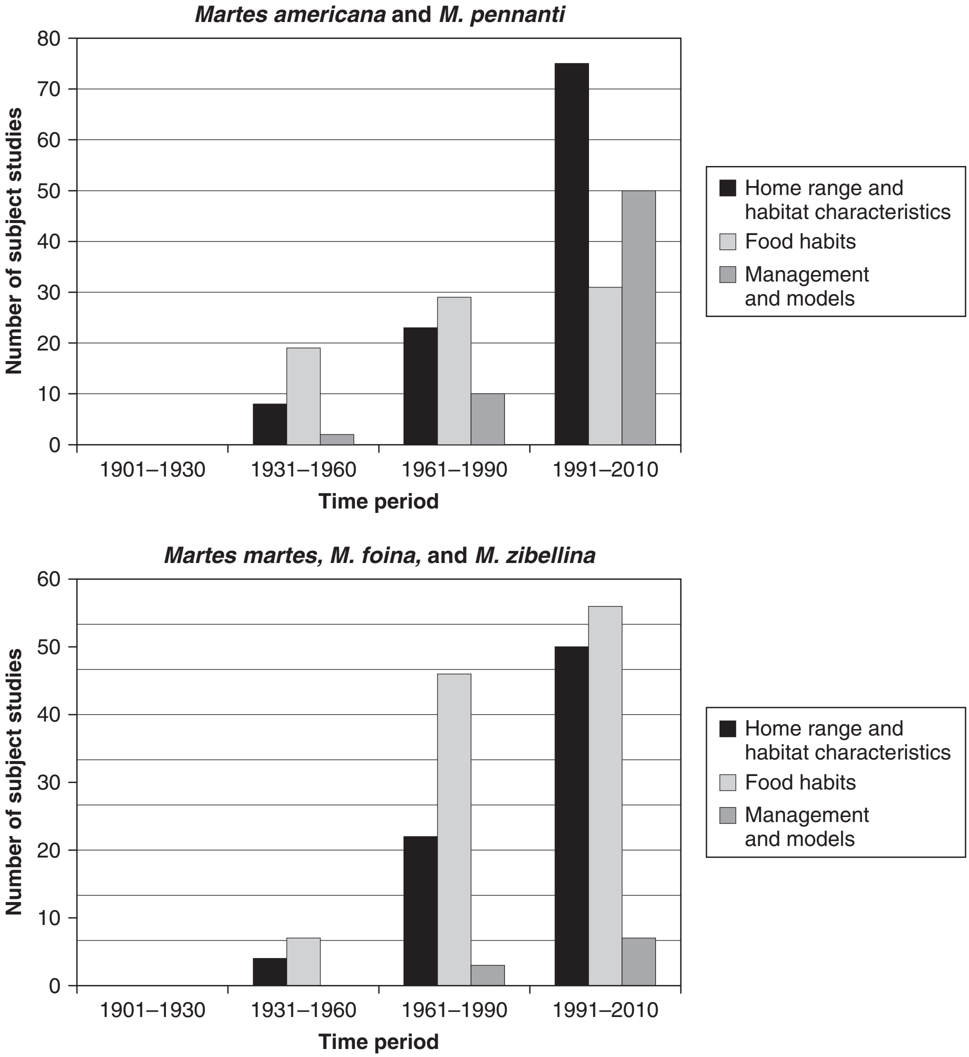

Figure 20.4. Frequency of subtopics for habitat studies by time period for *Martes* species.

expected from 1961 to 1990 and 1991 to 2010 for Group 1, and from 1991 to 2010 for Group 2 (Figure 20.2). For Group 1, the greater frequency of studies after 1960 was due largely to a marked increase in research on morphometry, physiology (e.g., thermoregulation, metabolic rate, body-fat dynamics), parasites, and diseases. For Group 2, more studies of morphometry and physiology were published after 1990.

Discussion

Changing Times

Martes research and management activities increased significantly from 1901 to 2010. We expected such a result, reflecting the evolution of the entire enterprise of science during the 20th century, that is, little scientific research, publication, and funding in the first half of the century, increased research activities and publications in the mid-1900s, when governments invested more in the advancement of science and technology, and constant annual growth in research, publications, and development programs after 1980 (Mabe and Amin 2001). Our results suggest that research themes for *Martes* species changed significantly at approximately 2 points in time: 1960 and 1990, resulting in 3 time periods during which the focus of *Martes* research and management was relatively consistent (Figure 20.5):

- 1901–1960: Utilitarian period. Research on *Martes* species was limited and included studies comprising mainly status and distribution reports.
- 1961–1990: Scientific period. This was a period of increased scientific interest in *Martes* species. In North America, studies on *Martes* populations and habitats increased, and significantly more work was conducted on the morphology, physiology, and behavior of species. In Europe and Asia, the number of publications on populations and the general biology of the species significantly increased.
- 1991–2010: Conservation period. During this period, research on *Martes* became much more management oriented. At the end of the 20th and beginning of the 21st centuries, public values and priorities for research and management were oriented toward the conservation of *Martes* populations and habitats. During this period, the number of publications on all subjects increased significantly.

Transitions from one period to the next did not occur abruptly (Figure 20.5). For example, although biologists were concerned about *Martes* populations, habitats, and harvests from 1961 to 1990 in North America, such concerns had been expressed during previous periods (e.g., Dixon 1925). Also, early thinking about wildlife management (Leopold 1933) and the factors that limit vertebrate populations (Errington 1946, 1956), along with the creation of scientific organizations such as The Wildlife Society (Bennitt et al. 1937) and the American Game Association (Allen 1985), paved the way for increased interest in research and management programs during the 1960s. In the 1950s, most biologists were interested primarily in the regional distribution of species (Dagg 1972), but some began to study population biology and habitat use. Thus, we could have set the beginning of the scientific period at

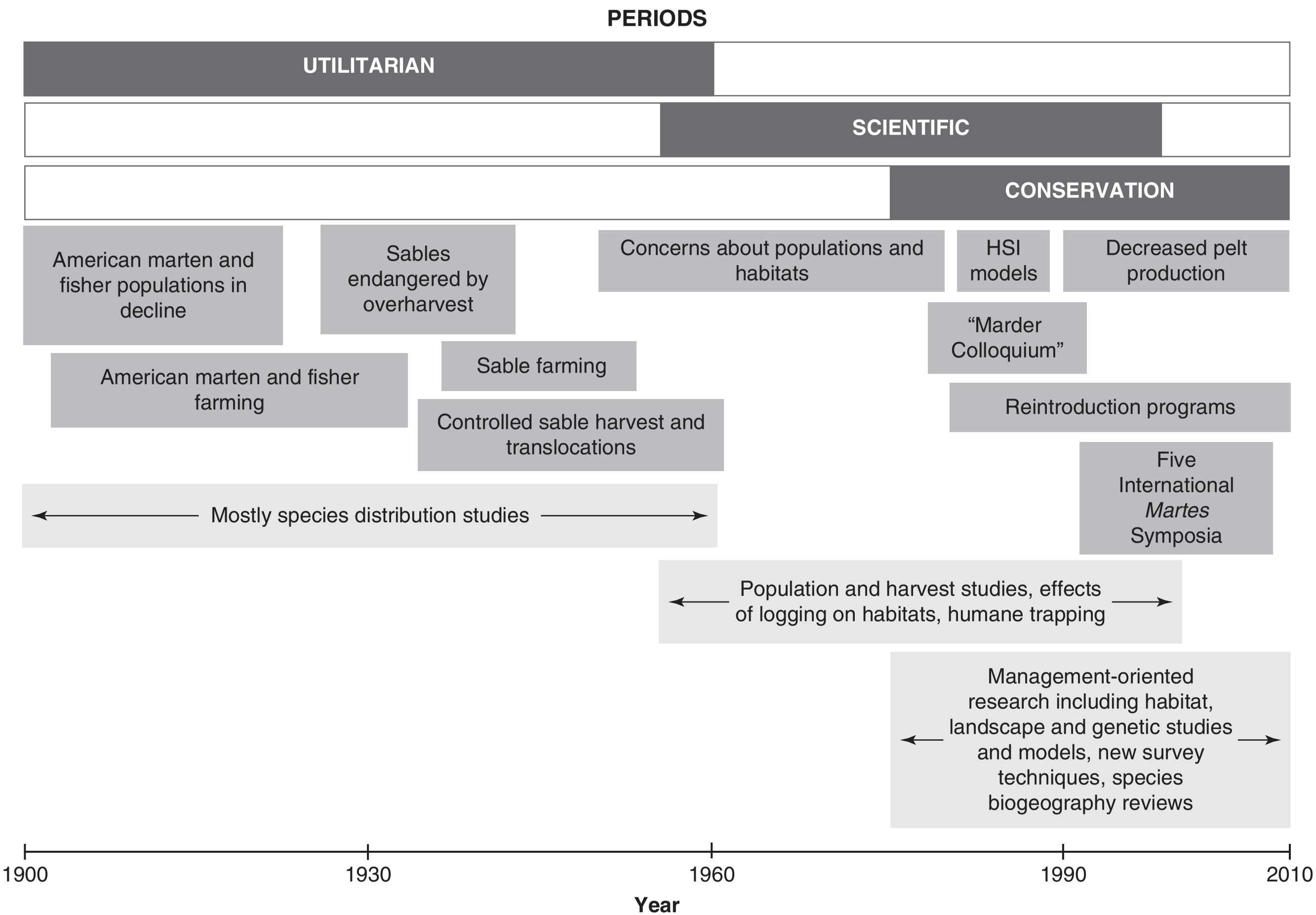

Figure 20.5. Schematic representation of chronological changes in *Martes* research and management from 1901 to 2010.

1950. It is important to realize that these themes were not exclusive to any one period, however; for example, many conservation activities began much earlier than 1991 (e.g., Anderson 1934).

1901–1960: Utilitarian Period

By the end of the 19th century, the genus *Martes* and its 3 subgenera (*Pekania*, *Charronia,* and *Martes*) had been established (Nowak 1999). At the beginning of the 20th century, the sable, the "black gold" of the early Middle Ages (Delort 1986), had been driven almost to extinction during the 1800s from overharvesting. Both European pine martens and stone martens were part of the fur trade in the early days and still being hunted at the beginning of the 20th century (Delort 1986; Bakeyev 1994; Proulx et al. 2004). In the 19th century, despite fluctuating prices (Ray 1987), pelts of American martens and fishers were consistently valuable (Innis 1956; Obbard et al. 1987). Interest in *Martes* species during the first half of the 20th century focused primarily on the value of martens, sables, and fishers as furbearing animals (Delort 1986; Proulx 2000); yet, they were trapped with little concern about resulting effects on wild stocks. At the beginning of the 20th century, the demand for raw furs was increasing, despite decreases in numbers (Gotlieb 1927). Our literature review indicated that although American martens and fishers were economically important furbearers, and their populations were in decline by the early 1900s (Dixon 1925; Dodds and Martell 1971), little field research was being conducted at that time. During the first half of the century, distributional assessments were most common (Dagg 1972).

Because of the value of *Martes* pelts and declining wild stocks, fur farming was attempted during the first half of the 20th century. Fur farming attained its greatest popularity during the 1920s as a thoroughly modern answer to the apparent and inevitable "exhaustion of nature" (Colpitts 1997). Sable farming began in the former Soviet Union in the late 1930s (Nes et al. 1988) and was successful (Korhonen et al. 2001). Fur farms for the American marten and fisher were also established in North America with some success (Jones 1913; Patton 1925; Hodgson 1937). However, their comparatively small litters, the long period before first parturition, and difficulties getting the animals to breed made farming of these species a risky business (Rand 1944; Douglas and Strickland 1987; Robitaille 2000).

Concurrent with the public demand for fur, researchers began investigating the reproductive biology of *Martes* species, including breeding (Reinhardt 1929; Ashbrook and Hanson 1930; Brassard and Bernard 1939), delayed implantation and gestation (Ashbrook and Hanson 1930; Wright 1942; Enders and Pearson 1943), and physiological and physical characteristics (Prell 1928; Brassard and Bernard 1939; Enders and Leekley 1941).

In the 1930s, a few scientists started showing some interest in the status of harvested populations. Anderson (1934: 4064) stated that "with every northern trapper after its pelt, unless the fisher becomes successfully acclimated on fur farms, this valuable species seems doomed to ultimate extinction." The status of the American marten was also in decline (Grinnell et al. 1937; Schorger 1942; Twining and Hensley 1947).

In 1935, active restoration of sable populations began with a 5-year ban on the hunting and sale of pelts in Yakutia and the Far East (Bakeyev and Sinitsyn 1994). This was followed by controlled harvests with quotas, and the development of farms where animals were bred in captivity to rebuild wild populations. From 1940 to 1965 in Russia, more than 19,000 sables were translocated into areas with low densities in the Far East and Yakutia, western Siberia and the Urals, and eastern and central Siberia (Bakeyev and Sinitsyn 1994). American martens and fishers benefited from the extensive establishment of registered traplines in Canadian provinces (Eklund 1946; Crichton 1948). In the United States, the establishment of annual harvest surveys and the closure of trapping seasons (Linhart 1985; Lewis and Zielinski 1996) also addressed conservation concerns.

By the early 1950s, wildlife managers knew that American martens and fishers were overharvested, and it had become imperative to learn more about harvested populations (Yeager 1950). Investigations showed that males and juveniles were more vulnerable to trapping than females or adults, respectively (Yeager 1950; Quick 1956); also, an equal sex ratio or one favoring females likely indicated overharvesting (Soukkala 1983; Archibald and Jessup 1984). By the mid-20th century, harvest management involved establishing quotas for registered traplines in Canada for each species, based on harvests during the preceding years. Although such an approach appeared satisfactory at the time (de Vos 1951b), later work suggested that it was unlikely to prevent overharvesting (Fortin and Cantin 1994). As Quick (1956: 271) pointed out, "the difficult problem of quantitatively measuring the effects of exploitation still demands a good appraisal of pre-season populations."

When conducting autecological studies, wildlife biologists began to explore factors other than trapping to explain declines in *Martes* populations. Researchers noticed that *Martes* species were associated with mature and old forests with dense cover, snags, and woody debris (de Vos 1952) and suggested that fire, logging, road building, mining, powerline clearing, and similar human activities were causing the disappearance of American martens and fishers from much of their range (Schmidt 1942; Yeager 1950; Miller et al. 1955; Lutz 1956), reflecting Seton's (1926: 206, 211) prediction that species "must disappear as the forest disappears."

1961–1990: Scientific Period

With the establishment of various research and management programs, the 1960s (and subsequent decades) represent a turning point for *Martes* management in North America (e.g., Anderson 1987; DiStefano 1987; Slough et al. 1987). This was also a time when public concerns about managing wildlife for consumptive uses resulted in more emphasis on environmental health and aesthetic values (Bolen 1989). In North America, American marten and fisher population levels had declined so much by 1950 (Yeager 1950; de Vos 1952) that government agencies throughout the continent initiated a number of reintroduction efforts (Table 20.1). From 1965 to 1993 in Russia, a captive-breeding population of 500 sables was established to restore the species in China (Ma and Xu 1994). European pine martens were also suffering the effects of habitat loss due to urbanization but had not yet been part of reintroduction programs.

Around 1950, biologists began to realize that there was a lack of information about factors affecting population densities and habitat carrying capacity (de Vos 1952). This realization initiated an era of studies on population dynamics (e.g., Hawley and Newby 1957), home ranges (e.g., Mech and Rogers 1977; Raine 1982; Wynne and Sherburne 1984), food habits (e.g., Cowan and Mackay 1950; Brown and Will 1979; Nagorsen et al. 1989), and the relations

Table 20.1. Reintroductions of American martens and fishers in North America from 1961 to 1990

Location	Reference
American marten	
Eastern and Central Canada	Rettie 1971; Bateman 1984; Sullivan 1984; Quann 1985; Sinclair 1986; Boss et al. 1987; Bissonette et al. 1988; Drysdale and Charlton 1988
Western Canada	Miller 1961; van Zyll de Jong 1969; Hobson et al. 1989
Canadian Territories	Slough 1994
Eastern United States	Soutiere and Coulter 1975
Midwest United States	Brander and Books 1973; Schupbach 1977; Churchill et al. 1981; Davis 1983; Gieck 1986; Fredrickson 1989
Western United States	Burris and McKnight 1973; Rognrud 1983
Fisher	
Eastern and Central Canada	Dodds and Martell 1971; Dilworth 1974
Western Canada	Davie 1984; Proulx et al. 1994
Eastern United States	Fuller 1975; Cottrell 1978; Pack and Cromer 1981; Wallace and Henry 1985
Midwest United States	Williams 1962a, 1963; Irvine et al. 1964; Petersen et al. 1977; Luque 1984; Kohn and Eckstein 1987
Western United States	Kebbe 1961a; Weckwerth and Wright 1968

among these subjects (e.g., Weckwerth and Hawley 1962; Zielinski et al. 1983; Thompson and Colgan 1987). These studies were accompanied by the development of new techniques to better determine the structure of populations (Parsons et al. 1978; Kuehn and Berg 1981; Strickland et al. 1982a). Armed with a better understanding of *Martes* populations, wildlife biologists revised harvest regulations to establish more realistic quotas (Strickland and Douglas 1981; Fortin and Cantin 1994; Garant et al. 1996) and implemented systematic trapper surveys (Lafond 1990). Despite improved harvest programs, the trapping of furbearers for economic gain and the use of archaic trapping devices became major public concerns. From the early 1980s to mid-1990s, the scientific community investigated and developed new trapping devices (Proulx 1999a) to increase capture efficiency and animal welfare. Traps that caused undue suffering were identified (Proulx et al. 1989b; Cole and Proulx 1994) and humane-trapping devices were developed according to new standards (Barrett et al. 1989; Proulx et al. 1989a; Proulx and Barrett 1994; Proulx 1997, 1999b).

From 1970 to 1990, the effects of logging on *Martes* were the subject of several investigations. Koehler and Hornocker (1977) and Pulliainen (1981b) observed limited use of openings by American martens and European pine martens, respectively. Large clear-cuts were repeatedly found to provide inadequate habitat for American martens in winter (Steventon and Major 1982; Snyder 1984). However, small clear-cuts interspersed with uncut forest stands and selectively cut stands were considered suitable for fishers (Allen 1983). Soutiere (1979) suggested that partial timber harvests that retained residual stands of 20–25 m^2/ha basal area in pole and larger trees were used by martens in winter. Similar findings were reported for fishers (Ingram 1973; Kelly 1977); however, later work would show that a change from clear-cutting to extensive partial harvesting can cause significant loss and fragmentation of American marten habitat (Fuller and Harrison 2005; Simons 2009).

In the western United States, Koehler et al. (1975) considered the American marten to be a "barometer" of the health of ecosystems that may provide clues to the effects of disturbances on other species, such as the fisher and woodland caribou (*Rangifer tarandus*). They also warned land managers that (1) during winter, martens need old-growth forests on mesic sites with canopy cover >30%; (2) martens rarely cross openings >100-m wide during the winter, and do not hunt in openings; and (3) mature-forest communities may support more martens in a given area, but a more diverse forest community will support more martens over time. They concluded that "managers could use logging to partially replace fire as an agent of diversity but mature forest communities must be maintained" (Koehler et al. 1975: 36).

In the early 1980s, new knowledge about American marten and fisher habitat use gave rise to untested habitat suitability index (HSI) models (Allen 1982, 1983). These models stressed the importance of tree-canopy closure and coniferous tree species for both American martens and fishers, whereas the successional stage of forest stands and the presence of abundant downfall (woody debris) were considered important to American martens only. HSI models were widely used by government agencies throughout North America, but because of regional variations in life-history parameters (including predation) and the poor quality of available vegetation data, they often generated questionable results (e.g., Laymon and Barrett 1986). By the end of the period from 1961 to 1990, biologists had concluded that American martens preferred dense, mature coniferous or mixed forests with high overstory cover (Francis and Stephenson 1972; Koehler et al. 1975; Douglas et al. 1983; Raine 1983; Bateman 1986). This turned out to be an overgeneralization, as later studies would show that in some areas, American martens were more closely associated with complex habitat structure than with particular forest age-classes (Potvin et al. 2000; Payer and Harrison 2003; Hearn et al. 2010). Nevertheless, although the reasons for the American marten's habitat preferences were still not clearly understood, other factors such as overhead cover from predation, prey abundance and availability, and thermoregulatory needs during winter appeared to be involved (Koehler and Hornocker 1977; Soutiere 1979; Buskirk et al. 1988; Bissonette et al. 1989).

In Europe, the 1980s were the turning point for research on *Martes*. In 1982, a "Marder Colloquium" took place in Germany, which was the first in an ongoing series of scientific meetings, including the 28th colloquium, held in The Netherlands in 2010. Originally, the goal of these meetings was to bring together biologists sharing an interest in martens, but later meetings included consideration of all mustelids, and the numbers of participants and countries represented have been growing steadily. In the 1980s, research conducted in Europe showed that the European pine marten and stone marten occupied a diversity of landscape conditions that differed from each other according to available habitat (e.g., Pulliainen 1981c; Clément and Saint-Girons 1982; O'Sullivan 1983; Marchesi and Mermod 1989) and prey (e.g., Marchesi et al. 1989). Intra- and interspecific studies (e.g., Pulliainen 1981c; Labrid 1987) were initiated to better understand population densities and distributions. Although the European pine marten was believed to be a woodland-dwelling mustelid (Pulliainen 1981c), the stone marten was associated with rural, urban, and forested habitats (Lodé 1991a). Despite a better understanding of habitat use by *Martes* species, patterns of habitat selection, the use of specific denning and resting sites, and animal movements across fragmented landscapes were still poorly understood at the end of the Scientific Period.

1991–2010: Conservation Period

During the last decade of the 20th century and the beginning of the 21st, the wildlife profession experienced changes in conservation values and public attitudes toward wildlife (Manfredo et al. 2003). As Salwasser (1995) noted, the world experienced the biodiversity crisis, the global-atmosphere crisis, the groundwater crisis, the urban-crime crisis, and the "you-name-it" crisis. As animal-rights activists raised concerns about the fur industry's practices, pelt production fell 62% in the early 1990s (Statistics Canada 2006), and the fur industry continued to struggle in the 2000s (Kozlov 2002; Trapping Today 2009). On the other hand, conservation biology and biodiversity assessment became exciting new research disciplines in the life sciences (Salafsky et al. 2002; Reid and Mace 2003).

In 1993, soon after the first International *Martes* Symposium was convened (Buskirk et al. 1994), the *Martes* Working Group (MWG) was created to facilitate communication among people with common interests in *Martes* research, conservation, and management programs. Thereafter, the MWG organized 3 additional symposia, and published the proceedings for each one (Proulx et al. 1997; Harrison et al. 2004; Santos-Reis et al. 2006).

Although our literature review suggested that research on the European pine marten, stone marten, and sable became increasingly important from 1961 to 1990, many papers on these species were published after 1991 on habitat and landscape selection (e.g., Pereboom et al. 2008; Sălek et al. 2009; Balestrieri et al. 2010; Herr et al. 2010; Vladimirova and Mozgovoy 2010), food habits (e.g., Jędrzejewski et al. 1993; Lachat-Feller 1993b; Brzeziński 1994; Buskirk et al. 1996a; Baltrūnaitė 2006a), and interspecific relations (e.g., Santos-Reis et al. 2004; Grassman et al. 2006b; Sidorovich et al. 2006), among other subjects.

As in Europe, *Martes* studies were numerous in North America from 1991 to 2010 (e.g., Coffin et al. 1997; Potvin and Breton 1997; Powell et al. 1997; Sturtevant and Bissonette 1997; Andruskiw et al. 2008). In this period of *Martes* history, biologists were faced with the challenge of understanding the conditions promoting population persistence, that is, what should be conserved, where, and how?

Habitat selection was the focus of many studies on *Martes* species from 1991 to 2010. Researchers conducted habitat-selection studies using forest-inventory data (Zielinski et al. 2006c, Proulx 2009), and both old and new techniques to detect the presence of *Martes* species (Zielinski and Kucera 1995; Aubry et al. 1997; Zielinski et al. 1997b; Poulton et al. 2006; Proulx and O'Doherty 2006; Rosellini et al. 2008). These and other studies reinforced the importance of forest structural complexity as a habitat predictor (Buskirk et al. 1996a; Miyoshi and Higashi 2005; Proulx 2006a). The prospect that fishers use cognitive maps as they make nonrandom use of space was also explored during this period (Powell 2000, 2004). Studies also stressed the potential effects of abiotic factors on *Martes* species (Krohn et al. 1997, 2004; Weir et al. 2004). This improved understanding of the habitat and landscape conditions occupied by *Martes* species allowed biologists to address a number of questions related to habitat selection and conservation. Habitat selection is, however, a complex process. All selection studies are relative, and they are especially sensitive to the habitat types (and other factors) that are present (or absent) in each study area. In addition, habitat use varies with such factors as prey type, prey abundance, forest structure, natural fragmentation, and the presence or absence of other carnivores (e.g., Hearn et al. 2010). Recognizing this complexity was a major research finding in itself. *Martes* researchers also developed spatially explicit population models to better predict trends under various environmental conditions (Carroll 2007).

To improve the management and conservation of *Martes* populations, biologists working in the Conservation Period also began to explore the genetics of species to better understand their biogeography and taxonomy, and to preserve genetic diversity (e.g., Hicks and Carr 1992; Carr and Hicks 1997; Koepfli et al. 2008). These data, together with studies on skeletal morphology (e.g., Reig 1992; Fortin et al. 1997; Monakhov 2010) led to discussions on subspecific taxonomy and the various factors that produce taxonomic variation (e.g., Nagorsen 1994; Bryant et al. 1997). Combining information about the distribution, spatial organization, and movements of animals with genotypic data enabled biologists to gain important new insights into the zoogeography and ecology of *Martes* populations (Kyle et al. 2000; Aubry et al. 2004; Pertoldi et al. 2008a). Reviews of the distribution and status of *Martes* populations became more comprehensive (Proulx et al. 2004), and biologists suggested that some populations were at risk or should be subject to further investigation to better conserve their habitats (Wisely et al. 2004; Álvares and Brito 2006; Matos and Santos-Reis 2006).

What's Next?

At the beginning of the 20th century, little was known about the populations and habitats of martens, sables, and fishers. Nearly 100 years later, researchers and wildlife managers know a great deal about the evolution, taxonomy, morphophysiology, genetics, population dynamics, habitat and predator-prey relations, food preferences, parasites, and diseases of most *Martes* species. This level of knowledge is particularly impressive when one considers that compared with large felids and canids, small carnivores receive relatively little attention from conservationists, researchers, government agencies, and funding sources (Schipper et al. 2009). Unfortunately, not all *Martes* species are well studied. Little is known about the yellow-throated marten in Southeast Asia (Proulx et al. 2004) or the Japanese marten in Japan and Korea (Saeki 2006), and almost nothing is known about the Nilgiri marten in southern India (Proulx et al. 2004). We urgently need new studies on these species that include the publication of research findings in scientific journals. It is hoped that research and development programs undertaken in North America and

Europe will be duplicated in those parts of the world where the ecological requirements of *Martes* populations are still relatively unknown.

The genera *Eira* and *Gulo* appear to form a clade with *Martes*; that is, their species possibly evolved from a common ancestor, or they may be sister lineages to a clade containing *Martes* (e.g., Koepfli et al. 2008; Hughes, this volume). Our understanding of the phylogenetic relations among the wolverine (*Gulo gulo*), tayra (*Eira barbara*), and *Martes* species will undoubtedly benefit from further investigations of mitochondrial and nuclear genes. Nevertheless, ecomorphological similarities among all these species should encourage *Martes* researchers to further investigate the ecological needs of these species when developing population and habitat conservation programs.

There is also a disparity between the amount of knowledge acquired by biologists, and the integration of such knowledge into wildlife-conservation programs. The ecology of most species is well known, and tools have been developed to identify important habitats that should be protected (Brainerd et al. 1994; Weir and Corbould 2008; Proulx 2009). Despite this knowledge, timber companies often adopt forest-management programs that do not properly address the needs of *Martes* species (Brainerd et al. 1994; Proulx 2009). For a forest-management plan to be effective for conserving *Martes* species, it must be based on spatially explicit data that relate to specific habitat requirements. Field work and improved forest-inventory data are needed to develop multiscale management programs that will address the needs of martens, sables, and fishers effectively. More work is also required to differentiate habitats that provide *Martes* species with optimal living conditions at times when survival depends on meeting unusually high energetic needs (e.g., winter, breeding season). More studies are needed at the microhabitat level to identify critical structural elements (if any), and to determine how and under which circumstances *Martes* use various portions of their home ranges. The movements and activities of predators and prey living in sympatry with *Martes* species should be studied under different environmental conditions, and at different phenological periods of *Martes* biology, to better understand habitat selection by martens, sables, and fishers within their home ranges, and why they may behave differently from one habitat type to another, or from one region to another. For example, predation by red foxes (*Vulpes vulpes*) may influence selection of resting and denning sites by European pine martens (Brainerd et al. 1995). Habitats with high densities of ground squirrels (*Spermophilus* spp.) are more important to American martens in summer, when the ground squirrels are active, than in winter when they hibernate and become inaccessible (Zielinski et al. 1983). Movements of American martens among habitats may be more linear and rapid along cut-block edges, but more tortuous in structurally complex forests (Heinemeyer 2002), where efficiencies in encountering and killing small mammals may be linked to higher abundance of coarse woody debris (Andruskiw et al. 2008).

In contrast to traditional population-genetic studies, modern landscape genetics provides a framework for investigating the influence of landscape elements and environmental features on gene flow, genetic discontinuities, and genetic population structure (Storfer et al. 2010; Schwartz et al., this volume). How dispersing martens navigate the landscape is still an unanswered question (Broekhuizen 2006). The combination of genetic and landscape-ecology tools creates an exciting field of research on *Martes* and other species that are sensitive to habitat loss and degradation (Virgós and García 2002; Gehring and Swihart 2003) and to potential dispersal barriers (e.g., roads; Grilo et al. 2009).

Martes conservation would benefit from integrating the needs of martens, sables, and fishers into multispecies conservation plans. Thomas et al. (1988) pointed out that numerous wildlife species in the western United States use old-growth forest disproportionately to its occurrence within their home ranges. These include the American marten, fisher, red tree vole (*Arborimus longicaudus*), northern flying squirrel (*Glaucomys sabrinus*), several species of bats, northern spotted owl (*Strix occidentalis caurina*), pileated woodpecker (*Dryocopus pileatus*), and many others. Thus, conserving the American marten and fisher would provide valuable habitat for many other species. Similarly, Proulx (2005a) integrated the habitat needs of the American marten and fisher with those of endangered species, such as the woodland caribou, wolverine, and grizzly bear (*Ursus arctos*), to identify areas supporting all these species where increased conservation efforts in landscapes managed for timber harvesting would benefit several species of concern. In the context of such a multispecies management program, *Martes* habitat and forest-succession models should be used to predict the location and spatial extent of suitable habitats, predict the outcomes of various forest-management scenarios, and assess the short- and long-term viability of *Martes* populations inhabiting landscapes that are vulnerable to climate change, support various predator and prey populations, and are subject to timber or fur harvests. Most importantly, models and management recommendations must be tested in replicated treatments under different conditions to learn more about *Martes* population needs and responses to various management scenarios. In particular, we need to determine whether habitat-management activities have fitness implications for *Martes* populations. Scientific research should not be separated from management activities, and management activities should not be carried out without proper scientific evaluation (Romesburg 1981; Sinclair 1991). On the other hand, the need to relate management activities to correlates of fitness should not delay the conservation of habitats shown in previous studies to be important to *Martes* species. In other words, we should not fail to implement what we know just because "we do not know it all."

Although the cumulative effects of hunting, trapping, and habitat loss may compromise the future of *Martes* populations (Banci and Proulx 1999;

Proulx and Verbisky 2001; Broekhuizen 2006), these factors have often been treated independently. In addition, despite the existence of new trapping technologies (Proulx 1999a) and standards (Proulx 1997; Powell and Proulx 2003), many wildlife researchers and trappers are unfamiliar with state-of-the-art trapping technology (Proulx et al. 2012). Older, less-humane trapping methods continue to be used; thus, *Martes* biologists must remain vigilant to ensure implementation of the best scientific and management practices in the field.

Despite several popular publications on the biology of martens and fishers (e.g., Haley 1975; Noblet 2002; Proulx 2010), we believe that most members of the general public know very little about *Martes* species. This is expected for species that are not only rare and elusive but also have a restricted geographic distribution (Wilson and Tisdell 2005; Aubry and Jagger 2006). To implement *Martes* conservation programs, however, wildlife professionals need the support of naturalist clubs, outdoor enthusiasts, and citizens from all walks of life. This need is particularly true where human development and economic growth impact biodiversity (Karmona 2007; Dawe and Mosley 2009). Agencies, companies, and individuals are often resistant to change and have difficulty adopting new findings and technologies. Change is also stymied by a lack of communication among *Martes* specialists, industry, and the public. Conserving *Martes* populations and their habitats is as much about changing human behavior as it is about collecting scientifically sound datasets. Reporting what we know to the public and finding win-win solutions between industrial interests and biologists will ultimately enhance the conservation of *Martes* populations and their habitats.

In the past, wildlife researchers have identified population- and habitat-management conflicts caused by agriculture, forestry, mining and oil exploration, and fur trapping (Proulx 2000). Unfortunately, little has been published on successful management programs and conflict resolutions, and examples of adaptive management for *Martes* conservation are scarce. Yet, *Martes* biologists in all parts of the world must deal with similar issues to conserve or restore threatened populations and habitats (Proulx et al. 2004). It is important to disseminate the results of both successful and unsuccessful management programs, so that other *Martes* biologists can improve their own programs and identify areas where more work is required to develop effective multiscale and multispecies programs for *Martes* management and conservation.

Acknowledgments

We express our gratitude to Bill Zielinski for his advice and editing work. We thank 2 anonymous referees for their critical review of an earlier version of the manuscript.