Chapter 1

THE *MARTES* COMPLEX: A MONOPHYLETIC CLADE THAT SHARES MANY LIFE-HISTORY TRAITS AND CONSERVATION CHALLENGES

Gilbert PROULX and Keith B. AUBRY

Abstract: Recent phylogenetic, phylogeographic, and morphometric studies have established the genetic affinities of the American marten (*Martes americana*), Pacific marten (*M. caurina*), European pine marten (*M. martes*), stone (beech, house) marten (*M. foina*), Japanese marten (*M. melampus*), yellow-throated marten (*M. flavigula*), Nilgiri marten (*M. gwatkinsii*), sable (*M. zibellina*), fisher (*Pekania pennanti*), wolverine (*Gulo gulo*), and tayra (*Eira barbara*). In this chapter, we evaluate the extent to which species in the *Martes* Complex share ecological adaptations and biological traits, and how such commonalities may be used for the conservation of species. Historical biogeography and recent research findings have shown that landscape connectivity was essential for species in the *Martes* Complex to avoid habitat isolation, and to maintain genetic connectivity through dispersal. Most species in the *Martes* Complex are associated with forests with high basal areas and large-diameter trees that provide complex vertical and horizontal structure, including snags and decaying trees, high volumes of fallen deadwood, and a well-developed understory. Denning and resting sites for species in the *Martes* Complex consist of tree cavities in large dead or live trees, hollow logs, rock crevices, burrows of other animals, and buildings. All species have a relatively broad food niche, which varies seasonally and annually depending on environmental conditions and food availability. Most species are polygamous, but the yellow-throated and Nilgiri martens are monogamous, and the tayra is likely promiscuous. They have a well-defined breeding season except for the subtropical and tropical tayra and yellow-throated marten, which have at least 2 oestruses/year. With the exception of the tayra, all exhibit delayed implantation of the blastocyst. Habitat loss and fragmentation, which may be caused by climate change, is the major threat endangering the persistence of species in the *Martes* Complex. The development of a conservation program to counteract habitat loss must first aim at the retention of landscapes with a

---

The *Martes* Complex in the 21st century: ecology and conservation, pages 3–24.
A. Zalewski, I.A. Wierzbowska, K.B. Aubry, J.D.S. Birks, D.T. O'Mahony, G. Proulx, editors;
2017, Mammal Research Institute, Polish Acadamy of Sciences, Białowieża, Poland

network of corridors interconnecting forest mosaics. These mosaics will provide species in the *Martes* Complex with forest stands, woodlots, and hedgerows containing complex vertical or horizontal structure that provide protection from predation and extreme temperatures, a diversified and abundant prey base, and secure denning and resting structures that provide thermoregulatory benefits and security for mothers and their young. A comprehensive evaluation of the ecological similarities among these species will require additional research.

INTRODUCTION

Recent phylogenetic, phylogeographic, and morphometric studies have provided compelling evidence that taxonomic revisions are needed to the genus *Martes* to resolve several long-standing issues. Numerous authors (e.g., Hosoda et al. 2000; Fulton and Strobeck 2006; Koepfli et al. 2008; Sato et al. 2012) have demonstrated that the genus *Martes* was paraphyletic with respect to the fisher (previously *M. pennanti*), and several recommended elevating the subgenus *Pekania* to generic status and reclassifying the fisher as *Pekania pennanti* (Koepfli et al. 2008; Sato et al. 2012). Recent publications on fishers in the primary literature (e.g., Aubry et al. 2013; Schwartz et al. 2013; Proulx and Dickson 2014) and in a recent update of the standard taxonomic checklist of North American mammals (Bradley et al. 2014) indicate that the scientific community has accepted this revision. In addition, the results of recent genetic studies on martens in North America raised long-standing questions about the appropriateness of recognizing only 1 species of marten in North America (the American marten [*M. americana*]; Carr and Hicks 1997; Stone and Cook 2002; Small et al. 2003). However, a recent synthesis of the taxonomic status of North American martens (Dawson and Cook 2012), using both morphometric and genetic data, showed that marten populations in southwestern North America (primarily the western contiguous United States and portions of coastal British Columbia) should be reclassified as the Pacific marten (*M. caurina*), while all other populations in North America should still be considered American martens. Recent journal publications (Moriarty and Epps 2015; Pauli et al. 2015), as well as the check list of North American mammals (Bradley et al. 2014), have also incorporated this taxonomic revision.

It is now understood that the genera *Martes, Pekania, Gulo,* and *Eira* belong to a monophyletic clade that reflects evolutionary divergence at the subfamily level (Hosoda et al. 2000; Fulton and Strobeck 2006; Koepfli et al. 2008; Sato et al. 2012). Wozencraft (1993) included these genera within the subfamily Mustelinae (which also included weasels and badgers, among others), but it is now clear that this subfamily is paraphyletic and also needs taxonomic revision (Sato 2016). Fulton and

Strobeck (2006) proposed that the clade which includes *Martes, Pekania, Gulo,* and *Eira* be given subfamilial status as Martinae, and this classification was followed by Koepfli et al. (2008), Larivière and Jennings (2009), and Yu et al. (2011). However, both Sato et al. (2012) and Li et al. (2014) placed these genera within the subfamily Guloninae in accordance with a recent evaluation of the correct nomenclature for some subfamilies in the Mustelidae (including Mustelinae) that provided support for using Guloninae, because it appears to be the oldest name proposed for this taxon (Nascimento 2014; Sato 2016).

In the absence of a widely accepted taxonomic designation for this new subfamily, Proulx and Aubry (2014) proposed using the term '*Martes* Complex' to describe the monophyletic clade that includes these 4 genera and comprises the following 11 extant species: American marten, Pacific marten, and fisher in northern North America; European pine marten (*M. martes*) and stone (beech, house) marten (*M. foina*) in Europe and south-central Asia; sable (*M. zibellina*) in northern and eastern Asia; Japanese marten (*M. melampus*) in Japan and the Korean Peninsula; yellow-throated marten (*M. flavigula*) in southeast Asia; Nilgiri marten (*M. gwatkinsii*) in southern India; wolverine (*Gulo gulo*) in tundra and boreal forests of Eurasia and North America; and tayra (*Eira barbara*) in southern Mexico, Central America, and northern South America (Presley 2000; Proulx et al. 2004; Copeland et al. 2010).

Both the fossil record and genetic evidence indicate that the genus *Martes* arose in moist tropical forests of southwest Eurasia during the middle or late Miocene (Hughes 2012; Li et al. 2014). The 11 extant species in this lineage evolved through a series of dispersals and speciations against a backdrop of cooling climates, sea level changes, mountain uplifts, aridification, and cyclical glacial events, all creating barriers to gene flow (Hughes 2012). Through the ages, species in the *Martes* Complex maintained their association with mesic environments (e.g., Hughes 2009), which may reflect their evolution from a Miocene ancestor that was adapted to the humid tropical and subtropical forests that covered southern Eurasia during the Miocene (Hughes 2012). True to the concept of phylogenetic niche conservatism, whereby species tend to retain their ancestral traits over time (Harvey and Pagel 1991; Holt and Gaines 1992; Wiens et al. 2010), all species in the *Martes* Complex retained their association with trees, i.e., they are semi-arboreal forest dwellers with sharp claws and long tails that provide a counter-balance when they are pursuing prey or travelling along branches (Larivière and Jennings 2009). Extant species in the *Martes* Complex occupy temperate boreal forests (American, Pacific, and European pine martens; sable; fisher; wolverine), coniferous-deciduous forests or hedges (pine and stone martens), and subtropical and tropical forests (yellow-throated, Japanese, and Nilgiri martens; tayra).

With the exception of the stone marten, all species in the *Martes* Complex are threatened to some degree by habitat loss (Proulx et al. 2004) and range fragmentation from climate change (Carroll 2007). Also, many species in the *Martes* Complex are at risk from habitat degradation (Proulx et al. 2004), including the European pine marten in several European countries; sable in China; Nilgiri marten in India; Japanese marten in Japan; American and Pacific martens in some Canadian provinces and American states; fisher in the Pacific coastal states; wolverine in Scandinavia (Persson et al. 2009) and the contiguous United States (U.S. Fish and Wildlife Service 2013); and tayra in some regions of Brazil (de Oliveira 2009).

Due to phylogenetic niche conservatism, closely related species tend to be similar ecologically (Losos 2008; Burns and Strauss 2011). However, no attempt has been made to identify commonalities in the ecological relations or life-history traits of the species in this phylogenetic clade. Such information could be extremely valuable for developing conservation programs that address common threats to the persistence of their populations. In this chapter, we evaluate the extent to which species in the *Martes* Complex share ecological adaptations and life history traits, and discuss how such commonalities could be used to improve efforts to conserve their populations.

LIFE-HISTORY TRAITS

Habitat associations at regional and landscape scales

The true martens (subgenus *Martes*; Hughes 2012) and the fisher (subgenus *Pekania*) occur exclusively in north-temperate boreal and montane regions (see maps in Proulx et al. 2004; Dawson and Cook 2012), whereas the yellow-throated marten (subgenus *Charronia*) occupies a wide variety of regions, including temperate, tropical, subalpine, and alpine environments (Appel and Khatiwada 2014). The Nilgiri marten (subgenus *Charronia*) and tayra occur in tropical and subtropical environments (see maps in Proulx et al. 2004; Cuarón et al. 2008), whereas wolverines primarily occupy tundra and boreal forests in the far north, and subalpine and alpine environments in temperate regions (Abramov et al. 2009). Despite intra- and inter-specific variation in the habitat types they use, all species in the *Martes* Complex are forest dwellers; i.e., they need the cover and protection of trees and the habitat conditions they provide during their daily activities or during particular phenological periods (Table 1.1).

The importance of forest cover for these species is clearly evident at the landscape scale. Occupancy by American martens in a forested landscape declines when 25–30% of the landscape is regenerating after timber harvest (Grakov 1972; Hargis et al. 1999; Potvin et al. 2000; Fuller and Harrison 2005). Typically, American and Pacific martens respond to habitat loss at the landscape scale by maintaining high-density populations in undisturbed forests (e.g., Chapin et al. 1997; Proulx 2009). Weir and Corbould (2010) suggested that the probability of a home range area being occupied by a resident fisher decreased with increasing amounts of open areas; i.e., a 5% increase in open areas within a potential home range decreased the probability of occupancy by 50%. European pine martens simply avoided clearcuts altogether (Brainerd 1997). Studies that investigated the movements, activity patterns, and habitat associations of species in the *Martes* Complex, even those of the generalist stone marten (Virgós and Garcia 2002), showed that martens, fishers, wolverines, and tayras were all associated with contiguous forest conditions (e.g., Badry et al. 1997; Pereboom et al. 2008; Proulx 2009). Wolverines use a variety of forested landscapes seasonally based on the availability of food, predation risk, and human disturbance (Hornocker and Hash 1981; Copeland et al. 2007; Krebs et al. 2007). However, successful reproduction and dispersal by wolverines requires contiguous areas of persistent spring snow cover (Magoun and Copeland 1998; Schwartz et al. 2009; Copeland et al. 2010), which may be compromised by climate change (Beniston 1997; Mote et al. 2005; McKelvey et al. 2011). Historical biogeography and recent research findings have shown that landscape connectivity was essential for species in the *Martes* Complex to avoid habitat isolation and promote gene flow through dispersal (Broquet et al. 2006; Garroway et al. 2011; Hughes 2012; Koen et al. 2012).

Habitat associations at forest stand and structure scales

Species in the *Martes* Complex are not dependent on any particular forest type for population persistence (e.g., Raley et al. 2012; Virgós et al. 2012). Fishers use a variety of forest types (Raley et al. 2012; Proulx 2017, this volume), and European pine and stone martens inhabit forests and woodlots characterized by a diversity of tree species (Virgós et al. 2012). In western montane regions, Pacific and American martens appear to prefer mature and old-growth coniferous forests (Mowat 2006; Slauson et al. 2007; Proulx 2009), but the American marten selects a broader array of forest types in eastern North America (Chapin et al. 1997; Hearn et al. 2010). Nevertheless, coniferous and mixedwood forests are particularly important to martens and fishers because they represent the best

Table 1.1. Habitats and den/rest sites of species in the *Martes* Complex.

Species	Geographic variation	Preferred habitat	Variants	Common features of occupied habitats	Den/rest sites	Source
Martes americana and *M. caurina*	Regional differences; variation in forest ages and types	Mature and old forests	Regenerating forests, burns, young deciduous stands, mosaics of seral stages	Forest cover and structural complexity at canopy and/or ground levels	Large dead or live trees, rock crevices, stumps, subnivean spaces	Ruggiero et al. 1998; Proulx et al. 2004; Thompson et al. 2012
M. martes	Broad range of landscape conditions including coniferous, deciduous, and Mediterranean forests	Undisturbed stands of older, mixed forests dominated by spruce; small wooded areas	Fragmented landscapes, and urban, suburban, and agricultural regions where the size of forest patches range from hedgerows (<1 ha) to woodlots (>100 ha)	Forest cover and structural complexity at canopy and/or ground levels	Tree cavities, rock crevices, buildings	Zalewski 1997; Brainerd and Rolstad 2002; Proulx et al. 2004; Birks et al. 2005; Pereboom et al. 2008; Balestrieri et al. 2010; Virgós et al. 2012
M. foina	Greater habitat generalization than other martens	Landscape mosaics with large forest patches	Use of buildings and car engine compartments in urban areas, rocky areas in fragmented habitats	Vertical and horizontal cover provided by forests, including small treed areas	Hollow trees, rock crevices, buildings	Proulx et al. 2004; Santos-Reis et al. 2004; Tóth et al. 2009; Virgós et al. 2012
M. zibellina	Regional differences	Mature and old coniferous forests	Forests with greater deciduous components in some regions	Forest cover and structural complexity at canopy and/or ground levels	Fallen deadwood	Ma and Xu 1994; Buskirk et al. 1996; Zhang and Ma 2000; Miyoshi and Higashi 2005

Table 1.1 – continued.

Species	Geographic variation	Preferred habitat	Variants	Common features of occupied habitats	Den/rest sites	Source
M. flavigula	Unknown	Tropical and subtropical forests, subalpine and alpine environments	Unknown	Unknown	Burrows, rock crevices	Proulx et al. 2004; Appel and Khatiwada 2014
M. melampus	Variable	Old deciduous and coniferous forests	Unknown	Unknown	Live trees, snags, burrows	Tatara 1994a
M. gwatkinsii	Unknown	Tropical rainforests with large trees	Unknown	Unknown	Possibly hollow trees	Balakrishnan 2005
Pekania pennanti	Differences among ecozones	Young, mature and old forests	Clearcuts, regenerating forests, mosaics of seral stages	Forest cover and structural complexity at canopy and/or ground levels	Large live trees, snags, decayed logs, subnivean spaces	Weir and Harestad 1997; Raley et al. 2012; Proulx 2017, this volume
Gulo gulo	Somewhat variable between boreal forest and tundra	Boreal forest and tundra communities where snow cover persists into the spring		Forest or shrubland cover	Snow caves, often in association with rocks or logs	Copeland and Whitman 2003; May et al. 2006; Copeland et al. 2010
Eira barbara	Highly variable	Dense tropical and subtropical forests	Gardens, plantations, dry scrub forests	Forest cover	Hollow logs or trees, beneath rocks, burrows	Presley 2000; Wainwright 2007; Goulart et al. 2009

combination of abundant food, access to well-insulated resting and denning sites, and reduced risk of predation (Storch et al. 1990; Fryxell et al. 1998; Kuriki et al. 1998; Orrlock et al. 2000; Brainerd and Rolstad 2002; Fuller et al. 2004; Elias et al. 2006; Cheveau et al. 2013).

Species in the *Martes* Complex are usually associated with forests containing high basal areas and large-diameter trees that provide complex vertical and horizontal structure, including snags and decaying trees, high volumes of fallen deadwood, and a well-developed understory (Table 1.1). Preferably, such forests have a large enough area to provide animals with interior forest conditions, i.e., sheltered, secluded environments away from the influence of forest edges and open habitats. All studies of denning and resting sites for species in the *Martes* Complex have reported the use of tree cavities in large dead or live trees, hollow logs, rock crevices, burrows of other animals, and buildings (Table 1.1). In addition, in northern regions during very cold temperatures, American martens, fishers, and wolverines seek subnivean refuges that provide thermoregulatory advantages (e.g., Copeland and Whitman 2003; Weir et al. 2004). All known denning and resting sites for this group of species provide both security cover and thermoregulatory benefits (Table 1.1).

Food habits

All species in the *Martes* Complex have a relatively broad food niche, which varies seasonally and annually depending on environmental conditions and food availability. Their diets consist of mammals, birds, vegetation, fruits, berries, nuts, mushrooms, invertebrates, and honey (e.g., Konecny 1989; Clevenger 1994; Presley 2000; McDonald 2002; Copeland and Whitman 2003; López-Martin 2006; May et al. 2006; Wainwright 2007). When seasonally abundant, fruits are a major dietary component for several species (e.g., European pine marten, Bermejo and Guitian 2000; stone marten, Pandolfi et al. 1996; yellow-throated marten, Zhou et al. 2008). Clevenger (1993a) reported that European pine martens fed mostly on grasshoppers in summer, but switched to fruits in the fall. In Spain, pine martens preyed almost exclusively on shrubland birds during the spring (Clevenger 1993b), but when microtine populations were low in the winter, they switched to alternative foods, such as berries and mushrooms (Pulliainen 1981). In the Canadian Rockies, wolverines use low-elevation forests inhabited by moose (*Alces alces*) during winter, but move to alpine areas and avalanche chutes in the summer to feed on marmots (*Marmota* spp.) and carrion (Krebs et al. 2007).

REPRODUCTION

Our understanding of the population biology of *Martes* Complex species is limited because they occur at low densities and have secretive behaviours; consequently, many have not been the subject of rigorous study (Aubry et al. 2012). Nevertheless, there are many similarities. Most species in the *Martes* Complex occupy temperate regions, are nocturnal and solitary in their activities, have a polygamous mating system, exhibit intrasexual territoriality, have a well-defined breeding season with delayed implantation of the blastocyst, average litter sizes ranging from 2–4, and parental care provided by the female without help from the male (Table 1.2). For temperate species, delayed implantation results in parturition occurring during the spring when environmental conditions are most favourable for raising young, and shifts the mating season away from the winter to a time when males are more mobile and can find receptive females (Larivière and Jennings 2009).

The Japanese marten, yellow-throated marten, Nilgiri marten, and tayra provide the only exceptions to these patterns, and are the only members of the *Martes* Complex that occupy tropical or subtropical regions. The reproductive ecology and territorial behaviour of Japanese martens are unknown. Yellow-throated and Nilgiri martens are diurnal and monogamous, and tayras are largely diurnal and are promiscuous breeders with multiple estruses each year, and they do not exhibit delayed implantation. Thus, seasonality in climatic conditions exerts a strong influence on reproductive and behavioural strategies among members of the *Martes* Complex.

CONSERVATION OF THE *MARTES* COMPLEX

Species in the *Martes* Complex share many life-history traits along an ecological spectrum. At one end of the spectrum is the wolverine, which is largely intolerant of human disturbance and infrastructures (May et al. 2006), requires large, undisturbed areas (Copeland and Whitman 2003), and depends on persistent spring snow cover for denning and successful reproduction (Copeland et al. 2010). At the other end is the stone marten, which is synanthropic, and uses the broadest range of habitats, including steppes, rocky areas, forests, and urbanized landscapes (Virgós et al. 2012). All other species in the *Martes* Complex fall somewhere between these extremes. Some species are allopatric (e.g., American and European martens), and others are sympatric (e.g., fisher, American marten, and wolverine; European pine and stone martens). Regardless of their position along this ecological spectrum, or overlap in their distributions,

Table 1.2. Reproductive traits of species in the *Martes* Complex based on information presented by Konecny (1989), Nowak (1991), Tatara (1994b), Presley (2000), Herr and Schley (2009), Larivière and Jennings (2009), Delgado-V. et al. (2011) Monakhov (2011), Buskirk et al. (2012), Shak (2012), Manzoor et al. (2013), and Appel and Khatiwada (2014).

Species	Mating system	Single, well-defined reproductive season?	Delayed implantation?	Litter size	Female raises young alone?	Intrasexual territoriality?	Diel activity pattern	Sociality
Martes americana and *M. caurina*	Polygamous	Yes	Yes	1–5, usually 2–3	Yes	Yes	Nocturnal and crepuscular	Solitary
M. martes	Polygamous	Yes	Yes	2–8, usually 2–3	Yes	Yes	Nocturnal	Solitary
M. foina	Polygamous	Yes	Yes	1–8, usually 3–4	Yes	Yes	Nocturnal	Solitary
M. zibellina	Polygamous	Yes	Yes	1–7, usually 3–4	Yes	Yes	Nocturnal and diurnal	Solitary
M. melampus	Unknown	Yes	Yes	Unknown	Yes	Unknown	Nocturnal	Unknown but probably solitary

Table 1.2 – continued.

Species	Mating system	Single, well-defined reproductive season?	Delayed implant-ation?	Litter size	Female raises young alone?	Intrasexual territoriality?	Diel activity pattern	Sociality
M. flavigula	Monogamous	No – 2 estruses/year	Yes	1–5, usually 2–3	Yes	Unknown	Diurnal	Travel in pairs or small family groups
M. gwatkinsii	Monogamous	Unknown	Yes	Unknown	Unknown	Unknown	Diurnal	Solitary but cases of pack hunting
Pekania pennanti	Polygamous	Yes	Yes	1–6, usually 2–3	Yes	Yes	Nocturnal and diurnal	Solitary
Gulo gulo	Polygamous	Yes	Yes	1–5, usually 2–4	Yes but male often visits young	Yes	Nocturnal	Solitary but related males may travel together
Eira barbara	Promiscuous	No – multiple estruses/year	No	1–3, usually 2	Yes	No	Diurnal and crepuscular	Solitary but adult pairs and small groups (females and their young) may be seen

all species in the *Martes* Complex are associated with trees and forests to some degree. In addition, all exhibit a preference for interconnected landscapes comprising forests in a variety of types and seral stages, and forests, woodlots, or hedges offering protection from predation and extreme environmental conditions. All members of the *Martes* Complex are threatened by habitat loss, which could impact their daily activities, food habits, movements, reproductive activities, and dispersal processes (Proulx et al. 2004; Ruggiero et al. 2007; de Oliveira 2009).

The development of a conservation program to address habitat losses must be focused on the retention or creation of landscapes that provide a network of travel corridors within a mosaic of forest conditions. Such mosaics contain complex vertical and horizontal structure that provides protection from predation and extreme temperatures and a diversified and abundant prey base, as well as secure denning and resting structures that confer additional thermoregulatory benefits and security for mothers and their young. Members of the *Martes* Complex prefer habitat stability to stochasticity. Forests with high structural complexity provide animals with a diversity of microhabitats that are resilient to variation in environmental conditions, and provide access to a diversified and abundant food base. In such habitats, when one type of food becomes scarce, martens, fishers, wolverines, and tayras can fall back on other items. A shift in the use of particular food items could not be accomplished as easily in simple environments, such as naturally regenerating forests, plantations without understories, monocultures, or forest stands with little or no structure near the ground.

In urban and suburban areas, the proportion of undisturbed land will likely be low. In such areas, the maintenance of natural corridors to facilitate animal movements within landscapes and provide potential denning and resting sites may benefit species such as the stone marten, which has flexible ecological requirements. In areas that are largely undisturbed (e.g., northern boreal forests, subalpine forests, alpine zones), protected areas may be needed as refugia, which could play an important role in the conservation of martens and fishers (e.g., de Vos 1951; Landa et al. 2000; Appel and Khatiwanda 2014), wolverines (e.g., Copeland and Whitman 2003; May et al. 2006), and tayras (Schreiber et al. 1989). Because species in the *Martes* Complex have relatively low reproductive rates (Table 1.2) and may have relatively large home ranges (Hornocker and Hash 1981; Weir and Corbould 2006), they have low resilience when habitat loss or alteration is coupled with high mortality rates from trapping, hunting, or poisoning (Banci and Proulx 1999; Gabriel et al. 2012). Large undisturbed areas (e.g., national parks, natural reserves) must be protected over the long term to ensure the growth and recovery of their populations (e.g., Buskirk et al. 2012).

The success (dispersal, survival, and settling) of populations of American martens (Johnson et al. 2009), fishers (Proulx and Dickson 2014), wolverines (Schwartz et al. 2009), and European pine martens (Broekhuizen 2006) are highly dependent on adequate connectivity within the landscapes they occupy, and it is probably true for other species in the *Martes* Complex. To provide for the integrity of populations and habitats over time, especially in light of potential threats to boreal species from global climate change, it may be most expedient to develop landscape management plans for an array of species where key habitats are identified and conserved for species in the *Martes* Complex and for species with similar ecological needs (e.g., Proulx 2005; Marcot and Raphael 2012).

CONCLUSIONS

In this chapter, we showed that there are enough similarities among preferred habitats for martens, fishers, wolverines, and tayras to identify common habitat features for the development of conservation programs that will provide benefits to members of the *Martes* Complex at multiple spatial scales. Due to these commonalities, biologists working on species in the *Martes* Complex would benefit from increased interactions (e.g., participating in international symposia convened by the *Martes* Working Group) to facilitate the development of collaborative efforts to conserve these species (Proulx and Aubry 2014). For example, a conservation strategy aimed at improving dispersal rates for 1 or more species of marten, would likely provide benefits to other species in the *Martes* Complex.

Understanding phylogenetic relationships among species in the *Martes* Complex took decades of work, and more studies are needed to fully understand those relationships. A comprehensive evaluation of the ecological similarities among these species will also require additional research. In particular, new studies on the tayra, yellow-throated marten, and Nilgiri marten will be needed to identify similarities in their behaviour and population dynamics in natural and human-altered ecosystems in tropical and subtropical regions. Finally, there is a need for additional research on the distributional ecology of species in the *Martes* Complex in relation to life-history traits, to better understand their habitat requirements, intraguild competition, and predation risk in various landscapes and habitat types. We hope that the ideas contained in this chapter will encourage other researchers to begin filling in some of these knowledge gaps.

ACKNOWLEDGMENTS

We thank 2 anonymous referees for helpful comments on an earlier version of this manuscript.

LITERATURE CITED

Abramov, A., J. Belant, and C. Wozencraft. 2009. *Gulo gulo*. The IUCN Red List of Threatened Species 2009. [http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T9561A13000870.en] Accessed 26 March 2016.

Appel, A., and A.P. Khatiwada. 2014. Yellow-throated martens *Martes flavigula* in the Kanchenjunga Conservation Area, Nepal. Small Carnivore Conservation 50:14–19.

Aubry, K.B., C.M. Raley, S.W. Buskirk, W.J. Zielinski, M.K. Schwartz, R.T. Golightly, K.L. Purcell, R.D. Weir, and J.S. Yaeger. 2013. Meta-analyses of habitat selection by fishers at resting sites in the Pacific coastal region. Journal of Wildlife Management 77:965–974.

Aubry, K.B., W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. 2012. Biology and conservation of martens, sables, and fishers: a new synthesis. Cornell University Press, Ithaca, New York, USA.

Badry, M.J., G. Proulx, and P.M. Woodard. 1997. Habitat use by fishers in the aspen parkland of Alberta. Pages 233–251 *in Martes*: taxonomy, ecology, techniques, and management. G. Proulx, H.N. Bryant, and P.M. Woodard, editors. Provincial Museum of Alberta, Edmonton, Canada.

Balakrishnan, P. 2005. Recent sightings and habitat characteristics of the endemic Nilgiri marten *Martes gwatkinsii* in western Ghats, India. Small Carnivore Conservation 33:14–16.

Balestrieri, A., L. Remonti, A. Ruiz-González, B.J. Gómez-Moliner, M. Vergara, and C. Prigioni. 2010. Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mammalian Biology 75:412–419.

Banci, V., and G. Proulx. 1999. Resiliency of furbearers to trapping in Canada. Pages 175–203 *in* Mammal trapping. G. Proulx, editor. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada.

Beniston, M. 1997. Variations of snow depth and duration in the Swiss Alps over the last 50 years: links to changes in large-scale climatic forcings. Climatic Change 36:281–300.

Bermejo, T., and J. Guitian. 2000. Fruit consumption by foxes and martens in NW Spain in autumn: a comparison of natural and agricultural areas. Folia Zoologica 49:89–92.

Birks, J.D.S., J. Messenger, and E.C. Halliwell. 2005. Diversity of den sites nsed by pine martens *Martes martes*: a response to the scarcity of arboreal cavities? Mammal Review 35:313–320.

Bradley, R.D., L.K. Ammerman, R.J. Baker, L.C. Bradley, J.A. Cook, R.C. Dowler, C. Jones, D.J. Schmidly, F.B. Stangl, Jr., R.A. Van Den Bussche, and B. Wursig. 2014. Revised checklist of North American mammals north of Mexico, 2014. Museum of Texas Tech University, Lubbock, USA.

Brainerd, S.M. 1997. Habitat selection and range use by the Eurasian pine marten (*Martes martes*) in relation to commercial forestry practices in southern boreal Scandinavia. PhD Thesis, Agricultural University of Norway, Aas, Norway.

Brainerd, S.M., and J. Rolstad. 2002. Habitat selection by Eurasian pine martens *Martes martes* in managed forest of southern boreal Scandinavia. Wildlife Biology 8:289–297.

Broekhuizen, S. 2006. *Martes* issues in the 21st century: lessons to learn from Europe. Pages 3–19 *in Martes* in carnivore communities. M. Santos-Reis, J.D.S. Birks, E.C. O'Doherty, and G. Proulx, editors. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada.

Broquet, T., N. Ray, E. Petit, J.M. Fryxell, and F. Burel. 2006. Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology 21:877–889.

Burns, J.H., and S.Y. Strauss. 2011. More closely related species are more ecologically similar in an experimental test. Proceedings of the National Academy of Sciences 108:5302–5307.

Buskirk, S.W., J. Bowman, and J.H. Gilbert. 2012. Population biology and matrix demographic modeling of American martens and fishers. Pages 77–92 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Buskirk, S.W., M. Yiqing, X. Li, and J. Zhaowen. 1996. Winter habitat ecology of sables (*Martes zibellina*) in relation to forest management in China. Ecological Applications 6:318–325.

Carr, S.M., and S.A. Hicks. 1997. Are there two species of martens in North America? Genetic and evolutionary relationships within *Martes*. Pages 15–28 *in Martes*: taxonomy, ecology, techniques, and management. G. Proulx, H.N. Bryant, and P.M. Woodard, editors. Provincial Museum of Alberta, Edmonton, Canada.

Carroll, C. 2007. Interacting effects of climate change, landscape conversion, and harvest on carnivore populations at the range margin: marten and lynx in the northern Appalachians. Conservation Biology 21:1092–1104.

Chapin, T.G., D.J. Harrison, and D.M. Phillips. 1997. Seasonal habitat selection by marten in an untrapped forest preserve. Journal of Wildlife Management 61:707–717.

Cheveau, M., L. Imbeau, P. Drapeau, and L. Bélanger. 2013. Marten space use and habitat selection in managed coniferous boreal forests of eastern Canada. Journal of Wildlife Management 77:749–760.

Clevenger, A.P. 1993a. Pine marten (*Martes martes* Linne, 1758) comparative feeding ecology in an island and mainland population in Spain. Zeitschrift für Säugetierkunde 58:212–224.

Clevenger, A.P. 1993b. Spring and summer food habits and habitat use of the European pine marten (*Martes martes*) on the island of Minorca, Spain. Journal of Zoology 229:153–161.

Clevenger, A.P. 1994. Feeding ecology of Eurasian pine martens and stone martens. Pages 326–340 *in* Martens, sables, and fishers: biology and conservation. S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Cornell University Press, Ithaca, New York, USA.

Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J.

Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88:233–246.

Copeland, J.P., J.M. Peek, C.R. Groves, W.E. Melquist, K.S. McKelvey, G.W. McDaniel, C.D. Long, and C.E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. Journal of Wildlife Management 71:2201–2212.

Copeland, J.P., and J.S. Whitman. 2003. Wolverine, *Gulo gulo*. Pages 672–682 *in* Wild mammals of North America. G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. Johns Hopkins University Press, Baltimore, Maryland, USA.

Cuarón, A.D., F. Reid, and K. Helgen. 2008. *Eira barbara*. IUCN Red List of Threatened Species 2008. [http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41644A10526741.en] Accessed 25 March 2016.

Dawson, N.G., and J.A. Cook. 2012. Behind the genes: diversification of North American martens (*Martes americana* and *M. caurina*). Pages 23–38 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Delgado-V., C.A., A. Árias-Alzate, S. Botero, and J.D. Sánchez-Londoño. 2011. Behaviour of the tayra *Eira barbara* near Medellín, Colombia: preliminary data from a video-capturing survey. Small Carnivore Conservation 44:19–21.

de Oliveira, T.G. 2009. Notes on the distribution, status, and research priorities of little-known small carnivores in Brazil. Small Carnivore Conservation 41:22–24.

de Vos, A. 1951. Overflow and dispersal of marten and fisher in Ontario. Journal of Wildlife Management 15:164–175.

Elias, S.P., J.P. Witham, and M.L. Hunter. 2006. A cyclic red-backed vole population and seedfall over 22 years in Maine. Journal of Mammalogy 87:440–445.

Fryxell, J.M., J.B. Falls, E.A. Falls, and R.J. Brooks. 1998. Long-term dynamics of small mammal populations in Ontario. Ecology 79:213–225.

Fuller, A.K., and D.J. Harrison. 2005. Influence of partial timber harvesting on American martens in north-central Maine. Journal of Wildlife Management 69:710–722.

Fuller, A.K., D.J. Harrison, and H.J. Lachowski. 2004. Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure. Forest Ecology and Management 191:373–386.

Fulton, T.L., and C. Strobeck. 2006. Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix analysis of multiple gene data sets. Molecular Phylogenetics and Evolution 41:165–181.

Gabriel, M.W., L.W. Woods, R. Poppenga, R.A. Sweitzer, C. Thompson, S.M. Matthews, J.M. Higley, S.M. Keller, K. Purcell, R.H. Barrett, G.M. Wengert, B.N. Sacks, and D.L. Clifford. 2012. Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare forest carnivore. PLOS ONE 7:e40163.

Garroway, C.J., J. Bowman, and P.J. Wilson. 2011. Using a genetic network to parameterize a landscape resistance surface. Molecular Ecology 20:3978–3988.

Goulart, F.V.L., N.C. Cáceres, M.E. Graipel, M.A. Tortato, I.R. Ghizoni, Jr., and L.G.R. Oliveira-Santos. 2009. Habitat selection by large mammals in a southern Brazilian Atlantic forest. Mammalian Biology 74:182–190.

Grakov, N.N. 1972. Effect of concentrated clearfellings on the abundance of pine marten (*Martes martes* L.) Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii 77:14–23. [In Russian with English summary]

Hargis, C.D., J.A. Bissonette, and D.L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157–172.

Harvey, P.H., and M.D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, UK.

Hearn, B.J., D.J. Harrison, A.K. Fuller, C.G. Lundrigan, and W.J. Curran. 2010. Paradigm shifts in habitat ecology of threatened Newfoundland martens. Journal of Wildlife Management 74:719–728.

Herr, J., and L. Schley. 2009. La fouine au Luxembourg. Ministère de l'Environnement, Le Gouvernement du Grand-Duché de Luxembourg, Luxembourg City. [In French]

Holt, R.D., and M.S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evolutionary Ecology 6:433–447.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59:1286–1301.

Hosoda, T., H. Suzuki, M. Harada, K. Tsuchiya, S.-H. Han, Y.P. Zhang, A.P. Kryukov, and L.K. Lin. 2000. Evolutionary trends of the mitochondrial lineage differentiation in species of genera *Martes* and *Mustela*. Genes & Genetic Systems 75:259–267.

Hughes, S.S. 2009. Noble marten (*Martes americana nobilis*) revisited: its adaptation and extinction. Journal of Mammalogy 90:74–92.

Hughes, S.S. 2012. Synthesis of *Martes* evolutionary history. Pages 3–22 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Johnson, C.A., J.M. Fryxell, I.D. Thompson, and J.A. Baker. 2009. Mortality risk increases with natal dispersal distance in American martens. Proceedings of the Royal Zoological Society of London B 276:3361–3367.

Koen, E.L., J. Bowman, C.J. Garroway, S.C. Mills, and P.J. Wilson. 2012. Landscape resistance and American marten gene flow. Landscape Ecology 27:29–43.

Koepfli, K-P., K.A. Deere, G.J. Slater, C. Begg, K. Begg, L. Grassman, M. Lucherini, G. Veron, and R.K. Wayne. 2008. Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biology 6:10.

Konecny, M.J. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. Pages 243–264 *in* Advances in neotropical mammalogy. K.H. Redford and J.F. Eisenberg, editors. Sandhill Crane Press, Gainesville, Florida, USA.

Krebs, J., E.C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2180–2192.

Kuriki, S., A. Nikula, P. Helle, and H. Lindén. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. Journal of Animal Ecology 67:874–886.

Landa, A., M. Lindén and I. Kojola. 2000. Action plan for the conservation of wolverines (*Gulo gulo*) in Europe. Nature and Environment, No. 115. Council of Europe Publishing, Strasbourg, France.

Larivière, S., and A.P. Jennings. 2009. Family Mustelidae (weasels and relatives). Pages 564–656 *in* Handbook of the mammals of the world. Volume 1. Carnivores. D.E. Wilson and R.A. Mittermier, editors. Lynx Edicions, Barcelona, Spain.

Li, B., M. Wolsan, D. Wu, W. Zhang, Y. Xu, and Z. Zeng. 2014. Mitochondrial genomes reveal the pattern and timing of marten (*Martes*), wolverine (*Gulo*), and fisher (*Pekania*) diversification. Molecular Phylogenetics and Evolution 80:156–164.

López-Martin, J.M. 2006. Comparison of feeding behavior between stone marten and common genet: living in coexistence. Pages 137–155 *in Martes* in carnivore communities. M. Santos-Reis, J.D.S. Birks, E.C. O'Doherty, and G. Proulx, editors. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada.

Losos, J.B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters 11:995–1007.

Ma, Y., and L. Xu. 1994. Distribution and conservation of sables in China. Pages 255–261 *in* Martens, sables, and fishers: biology and conservation. S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Cornell University Press, Ithaca, New York, USA.

Magoun, A., and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62:1313–1320.

Manzoor, M., A. Riaz, Z. Iqbal, and A. Mian. 2013. Biodiversity of Pir Lasura National Park, Azad Jammu and Kashmir, Pakistan. Science, Technology and Development 32:182–196.

Marcot, B.G., and M.G. Raphael. 2012. Conservation of martens, sables, and fishers in multispecies bioregional assessments. Pages 451–470 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

May, R., A. Landa, J. van Dijk, J.D.C. Linnell, and R. Andersen. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. Wildlife Biology 12:285–295.

McDonald, R.A. 2002. Resource partitioning among British and Irish mustelids. Journal of Animal Ecology 71:185–200.

McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littell, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. Ecological Applications 21:2882–2897.

Miyoshi, K., and S. Higashi 2005. Home range and habitat use by the sable *Martes zibellina brachyuran* in a Japanese cool-temperate mixed forest. Ecological Research 20:95–101.

Monakhov, V.G. 2011. *Martes zibellina* (Carnivora: Mustelidae). Mammalian Species 43:75–86.

Moriarty, K.M., and C.W. Epps. 2015. Retained satellite information influences performance of GPS devices in a forested ecosystem. Wildlife Society Bulletin 39:349–357.

Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86:39–49.

Mowat, G. 2006. Winter habitat associations of American martens *Martes americana* in interior wet-belt forests. Wildlife Biology 12:51–61.

Nascimento, F.O. 2014. On the correct name to use for some subfamilies of Mustelidae (Mammalia, Carnivora). Papeis Avulsos de Zoologia 54:307–313.

Nowak, R.M. 1991. Walker's mammals of the world. Vol. II. Fifth edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Orrlock, J.L., J.F. Pagels, W.J. McShea, and E.K. Harper. 2000. Predicting presence and abundance of small mammal species: the effect of scale and resolution. Ecological Applications 10:1356–1366.

Pandolfi, M., A.M. De Marinis, and I. Petrov. 1996. Fruit as a winter feeding resource in the diet of stone marten (*Martes foina*) in east-central Italy. Zeitschrift für Säugetierkunde 61:215–220.

Pauli, J.N., W.E. Moss, P.J. Manlick, E.D. Fountain, R. Kirby, S.M. Sultaire, P.L. Perrig, J.E. Mendoza, J.W. Pokallus, and T.H. Heaton. 2015. Examining the uncertain origin and management role of martens on Prince of Wales Island, Alaska. Conservation Biology 29:1257–1267.

Pereboom, V., M. Mergey, N. Villerette, R. Helder, J.-F. Gerard, and T. Lodé. 2008. Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. Canadian Journal of Zoology 86:983–991.

Persson, J., G. Ericsson, and P. Segerström. 2009. Human caused mortality in the endangered Scandinavian wolverine population. Biological Conservation 142:325–331.

Potvin, F., L. Bélanger, and K. Lowell. 2000. Marten habitat selection in a clearcut boreal landscape. Conservation Biology 14:844–857.

Presley, S.J. 2000. *Eira barbara*. Mammalian Species 636:1–6.

Proulx, G. 2005. Integrating the habitat needs of fine- and coarse-filter species in landscape planning. Pages 1–31 *in* Proceedings of the Species at Risk 2004 Pathways to Recovery Conference. T.D. Hooper, editor. B.C. Species at Risk 2004 Pathways to Recovery Conference Organizing Committee, Victoria, B.C., Canada.

Proulx, G. 2009. Conserving American marten *Martes americana* winter habitat in sub-boreal spruce forests affected by mountain pine beetle *Dendroctonus ponderosae* infestations and logging in British Columbia, Canada. Small Carnivore Conservation 41:51–57.

Proulx, G. 2017. Late-winter habitat of fisher (*Pekania pennanti*) in 3 ecozones of western Canada: implications for habitat conservation. Pages 249–260 *in* The *Martes* Complex in the 21st century: ecology and conservation. A. Zalewski, I.A. Wierzbowska, K.B. Aubry, J.D.S. Birks, D.T. O'Mahony, and G. Proulx, editors. Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.

Proulx, G., and K.B. Aubry. 2014. The "*Martes* Complex" – an opportunity to bring together marten, fisher, sable, wolverine, and tayra biologists. Canadian Wildlife Biology & Management 3:30–33.

Proulx, G., K. Aubry, J. Birks, S. Buskirk, C. Fortin, H. Frost, W. Krohn, L. Mayo, V. Monakhov, D. Payer, M. Saeki, M. Santos-Reis, R. Weir, and W. Zielinski. 2004. World distribution and status of the genus *Martes* in 2000. Pages 21–76 *in* Martens and fishers (*Martes*) in human-altered landscapes: an international perspective. D.J. Harrison, A.K. Fuller, and G. Proulx, editors. Springer Science+Business Media, New York, USA.

Proulx, G., and H.L. Dickson. 2014. Occurrence and distribution of fishers (*Pekania pennanti*) in the central aspen parklands of Alberta. Canadian Wildlife Biology & Management 3:15–21.

Pulliainen, E. 1981. Food and feeding habits of the pine marten in a Finnish Lapland forest in winter. Pages 580–598 *in* Worldwide Furbearer Conference Proceedings. J.A. Chapman and D. Pursley, editors. Worldwide Furbearer Conference, Frostburg, Maryland, USA.

Raley, C.M., E.C. Lofroth, R.L. Truex, J.S. Yaeger, and J.M. Higley. 2012. Habitat ecology of fishers in western North America. Pages 231–254 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Ruggiero, L.F., K.S. McKelvey, K.B. Aubry, J.P. Copeland, D.H. Pletscher, and M.G. Hornocker. 2007. Wolverine conservation and management. Journal of Wildlife Management 71:2145–2146.

Ruggiero, L.F., D.E. Pearson, and S.E. Henry. 1998. Characteristics of American marten den sites in Wyoming. Journal of Wildlife Management 62:663–673.

Santos-Reis, M., M.J. Santos, S. Lourenço, J.T. Marques, I. Pereira, and B. Pinto. 2004. Relationships between stone martens, genets and cork oak woodlands in Portugal. Pages 147–172 *in* Martens and fishers (*Martes*) in human-altered environments: an international perspective. D.J. Harrison, A.K. Fuller, and G. Proulx, editors. Springer Science+Business Media, New York, USA.

Sato, J.J. 2016. Systematics and taxonomy of the world's badger species – a review. Pages 1–30 *in* Badgers: systematics, biology, conservation and research techniques. G. Proulx and E. Do Linh San, editors. Alpha Wildlife Publications, Sherwood Park, Alberta, Canada.

Sato, J.J., M. Wolsan, F.J. Prevosti, G. D'Elía, C. Begg, K. Begg, T. Hosoda, K.L. Campbell, and H. Suzuki. 2012. Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). Molecular Phylogenetics and Evolution 63:745–757.

Schreiber, A., R. Wirth, M. Riffel, and H. Van Rompaey. 1989. Weasels, civets, mongooses, and their relatives. An action plan for the conservation of mustelids and viverrids. IUCN, Gland, Switzerland.

Schwartz, M.K., J.P. Copeland, N.J. Anderson, J.R. Squires, R.M. Inman, K.S. McKelvey, K.L. Pilgrim, L.P. Waits, and S.A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology 90:3222–3232.

Schwartz, M.K., N.J. DeCesare, B.S. Jimenez, J.P. Copeland, and W.E. Melquist. 2013. Stand- and landscape-scale selection of large trees by fishers in the Rocky Mountains of Montana and Idaho. Forest Ecology and Management 305:103–111.

Shak, M. 2012. *Martes flavigula*. Animal Diversity Web. [http://animaldiversity.org/accounts/Martes_flavigula/] Accessed 9 May 2016.

Slauson, K.M., W.J. Zielinski, and J.P. Hayes. 2007. Habitat selection by American martens in coastal California. Journal of Wildlife Management 71:458–468.

Small, M.P., K.D. Stone, and J.A. Cook. 2003. American marten (*Martes americana*) in the Pacific Northwest: population differentiation across a landscape fragmented in time and space. Molecular Ecology 12:89–103.

Stone, K.D., and J.A. Cook. 2002. Molecular evolution of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae). Molecular Phylogenetics and Evolution 24:169–179.

Storch, I., E. Lindström, and J. de Jounge. 1990. Diet and habitat selection of the pine marten in relation to competition with the red fox. Acta Theriologica 35:311–320.

Tatara, M. 1994a. Ecology and conservation status of the Tsushima marten. Pages 272–279 *in* Martens, sables, and fishers: biology and conservation. S.W. Buskirk, A.S. Harestad, M.G. Raphael, and R.A. Powell, editors. Cornell University Press, Ithaca, New York, USA.

Tatara, M. 1994b. Notes on the breeding ecology and behavior of Japanese martens on Tsushima Islands, Japan. Journal of the Mammalogical Society of Japan 19:67–74.

Thompson, I.D., J. Fryxell, and D.J. Harrison. 2012. Improved insights into use of habitat by American martens. Pages 209–230 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Tóth, M., A. Bárány, and R. Kis. 2009. An evaluation of stone marten (*Martes foina*) records in the city of Budapest, Hungary. Acta Zoologica Academiae Scientiarum Hungaricae 55:199–209.

U.S. Fish and Wildlife Service. 2013. Endangered and threatened wildlife and plants; threatened status for the distinct population segment of the North American wolverine occurring in the contiguous United States. Federal Register 78:7864–7890.

Virgós, E., and F.J. Garcia. 2002. Patch occupancy by stone martens *Martes foina* in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. Acta Oecologia 23:231–237.

Virgós, E., A. Zalewski, L.M. Rosalino, and M. Mergey. 2012. Habitat ecology of *Martes* species in Europe. Pages 255–266 *in* Biology and conservation of martens, sables, and fishers: a new synthesis. K.B. Aubry, W.J. Zielinski, M.G. Raphael, G. Proulx, and S.W. Buskirk, editors. Cornell University Press, Ithaca, New York, USA.

Wainwright, M. 2007. The mammals of Costa Rica. Cornell University Press, Ithaca, New York, USA.

Weir, R.D., and F.B. Corbould. 2006. Density of fishers in the sub-boreal spruce biogeoclimatic zone of British Columbia. Northwestern Naturalist 87:118–127.

Weir, R.D., and F.B. Corbould. 2010. Factors affecting landscape occupancy by fishers in north-central British Columbia. Journal of Wildlife Management 74:405–410.

Weir, R., F. Corbould, and A. Harestad. 2004. Effect of ambient temperature on the selection of rest structures by fishers. Pages 187–197 *in* Martens and fishers (*Martes*) in human-altered environments: an international perspective. D.J. Harrison, A.K. Fuller, and G. Proulx, editors. Springer Science+Business Media, New York, USA.

Weir, R.D., and A.S. Harestad. 1997. Landscape-level selectivity by fishers in south-central British Columbia. Pages 252–264 *in Martes*: taxonomy, ecology, techniques, and management. G. Proulx, H.N. Bryant, and P.M. Woodard, editors. Provincial Museum of Alberta, Edmonton, Canada.

Wiens, J.J., D.D. Ackerly, A.P. Allen, B.L. Anacker, L.B. Buckley, H.V. Cornell, E.I. Damschen, T.J. Davies, J.-A, Grytnes, S.P. Harrison, B.A. Hawkins, R.D. Holt, C.M. McCain, and P.R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13:1310–1324.

Wozencraft, W.C. 1993. Carnivora. Pages 279–348 *in* Mammal species of the world: a taxonomic and geographic reference. Second edition. D.E. Wilson and D.M. Reeder, editors. Smithsonian Institution Press, Washington, D.C., USA.

Yu, L., D. Peng, J. Liu, P. Luan, L. Liang, H. Lee, M. Lee, O.A. Ryder, and Y.-P. Zhang. 2011. On the phylogeny of Mustelidae subfamilies: analysis of seventeen nuclear non-coding loci and mitochondrial complete genomes. BMC Evolutionary Biology 11:92.

Zalewski, A. 1997. Factors affecting selection of resting site type by pine marten in primeval deciduous forests (Białowieża National Park, Poland). Acta Theriologica 42:271–288.

Zhang, H., and J. Ma. 2000. A preliminary study on the habitat selection of sable (*Martes zibellina)* in the autumn. Acta Ecologica Sinica 20:150–154.

Zhou, Y.-B., E. Slade, C. Newman, X-M. Wang, and S.-Y. Zhang. 2008. Frugivory and seed dispersal by the yellow-throated marten, *Martes flavigula,* in a subtropical forest of China. Journal of Tropical Ecology 24:219–223.