MARTENS AND FISHERS *(MARTES)* IN HUMAN-ALTERED ENVIRONMENTS:

An International Perspective

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An American marten pursuing its most common prey, the red-backed vole. Drawing by Mark McCollough.

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This book is dedicated
to
John “Jack” McPhee
1937–2003
Long-Time Telemetry Pilot, Naturalist, and Friend

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PREFACE

The genus *Martes* represents 7 species in the family Mustelidae, including 6 species of martens and the fisher *(M. pennanti),* who are phylogenetically and ecologically distinct from other weasels, minks, otters, and badgers. Other members of the genus include the pine marten *(M. martes)* and the stone marten *(M.foina)* of Europe and Asia, the sable *(M. zibellina)* of northern Asia, the Korean peninsula, and some islands of the Japanese archipelago, the indigenous Japanese marten *(M. melampus)* of Japan and the Korean peninsula, the American marten *(M. americana)* of the northern United States and Canada, and the little studied yellow-throated marten *(M. flavigula)* of Asia. As the taxonomic relationship between the yellow-throated marten of southern and southeastern Asia and the Nilgiri marten *(M. gwatkinsi)* of the Indian subcontinent remains questionable, we have taken a conservative taxonomic approach and consider them here as the same species.

All *Martes* have been documented to use forested habitats and 6 species (excluding the stone marten) are generally considered to require complex mid- to late-successional forests throughout much of their geographic ranges. All species in the genus require complex horizontal and vertical structure to provide escape cover, protection from predators, habitat for their prey, access to food resources, and protection from the elements. Martens and the fisher have high metabolic rates, have large spatial requirements, have high surface area to volume ratios for animals that often inhabit high latitudes, and often require among the largest home range areas per unit body weight of any group of mammals. Resulting from these unique life history characteristics, this genus is particularly sensitive to human influences on their habitats, including habitat loss, stand-scale simplification of forest structure via some forms of logging, and landscape-scale effects of habitat fragmentation. Given their strong associations with structural complexity in forests, martens and the fisher are often considered as useful barometers of forest health and have been used as ecological indicators, flagship, and umbrella species in different parts of the world, particularly in the United States, Canada, and Scandinavia. Thus, efforts to successfully conserve and manage martens and fishers are associated with the ecological fates of other forest dependent species and can greatly influence ecosystem integrity within forests that are increasingly shared among wildlife and humans.

Human populations continue to increase exponentially at the global scale and less than 7% of the world's land area is protected. Further, many protected areas within the range of the world's *Martes* experience managed and unmanaged forms of direct exploitation of these species and their habitats. Martens and the fisher often live in landscapes where harvesting of wood and extraction of minerals and energy resources provide the most significant economic returns. Further, these species live in complex and ever-changing ecological communities where their interspecific interactions, food resources, and habitat structure are affected by global processes such as international wood fiber markets and climate change. If viable populations of these species are to exist outside of the scarce inviolate parks and reserves scattered throughout the globe, then humans are challenged to understand the functional effects of their activities at the level of the individual and population and at multiple spatial scales ranging from the microhabitat, patch, landscape, and the metapopulation.

Historically, martens and the fisher (with the possible exclusion of the stone marten who has adapted to take advantage of the unnatural structural complexity, cover, and food resources that are enhanced in some human-dominated landscapes) have been associated with forested areas with low human populations. This has contributed to a general perception that these species are intolerant to humans and cannot adapt to human alterations of their habitat. Indeed, recent research has indicated that these species, which are often considered valuable furbearers, are vulnerable to over-exploitation and changes in population structure associated with overharvesting, increased access for humans via forest roads and trails, and indiscriminate killing. The American marten and the fisher were extirpated throughout many remote areas of North America during the late 1800s and early 1900s as a result of unregulated trapping and shooting for their furs, despite that other habitat conditions remained favorable. These species have been subsequently restored to many areas of their former range despite increasing human populations and access; many of these populations again support sustainable, regulated harvests in habitats significantly altered by humans. Thus, one of our primary challenges is to understand the resiliency and limits of *Martes* populations to sustain human-caused forms of mortality.

The historical (pre-1985) literature also focused on the stand-scale associations of martens and the fisher with mature and over-mature forests and of the relationship of these species with pristine forests. Recent studies in both North America and Europe have indicated that the relationships of Martes with humans may be more complex than previously understood. Martens and the fisher have been documented to use a range of forest types and seral stages throughout their geographic ranges; however, unifying principles supporting the requirement for complex horizontal and vertical structure are emerging. Recent studies have reported *Martes* successfully co-existing in some areas with human activities such as logging; these examples provide promising evidence that our increasing knowledge may be used (in some places) to mitigate human influences on habitat, and to provide opportunities for these species to co-exist in some landscapes altered by humans. New knowledge also suggests that broad-scale processes such as fragmentation of habitat across landscapes increasingly threaten the world's *Martes,* and that processes such as climate change may threaten the integrity of the natural communities where these species interact with a multitude of the world's flora and fauna. Again, our challenge is to understand the conditions where humans and martens are compatible and incompatible, and to promote land use practices that allow *Martes* to be representatively distributed and viable.

The 14 chapters of this book address I) the status, distribution, and life history of martens (7 species) throughout the world; II) the habitat and interspecific relationships relationships (3 species) at multiple spatial scales in North America and Europe; and III) new management and research approaches for evaluating and studying martens, the fisher, and their habitats. All of these papers provide tools and insights for better understanding *Martes* in landscapes that are significantly altered by humans. Monumental gaps continue to exist that hinder our understanding of the relationships of humans with some species, most notably the Japanese marten and yellow-throated marten. In the past 2 decades we have made great strides in our fundamental understanding of how animals with these unique life history traits perceive and utilize habitats, respond to habitat change, and how their populations function and perform under different forms of human management and mismanagement. Hopefully this knowledge will enhance our basic understanding of all species of *Martes* and will help us to achieve the goal of conserving viable populations and representative distributions of the world's *Martes,* their habitats, and associated ecological communities in our new millennium.

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Part I

Status, Distribution, and Life History

Chapter 1

IS MUSTELID LIFE HISTORY DIFFERENT?

Steven Ferguson and Serge Larivière

Abstract: The relationship between life-history variation and population processes may form a foundation for developing conservation strategies. Researchers have argued that mustelids require special conservation practices due to their unique habitat requirements and K-selected life-history strategy. We used the comparative method to test whether life-history and behavioral traits of mustelids differed from those of other carnivores. Controlling for phylogeny, we documented that mustelids are characterized by shorter gestation ($P = 0.09$) relative to other terrestrial carnivores. Moreover, mustelids have a longer period of estrus, and are more sexually dimorphic, live at lower densities, and occupy larger home ranges. The amount of energy (evapotranspiration) did not differ between the environments of mustelids and other carnivores, but mustelids lived with greater variation in energy (seasonality). We argue that mustelids have evolved "bet-hedging" life-history adaptations to unpredictable environments that include a trade-off between adult survival and reproductive effort. Thus, conservation measures to promote persistence of mustelid populations should consider environmental unpredictability, and ensure low trapping rates of adults.

1. INTRODUCTION

Environmental complexity (Gittleman 1986) and high seasonality (King 1980) may characterize the environment in which mustelidae (hereafter referred to as mustelids) evolved, and hence may help explain differences in life histories relative to other carnivores. Terrestrial mustelids (excludes mink *Mustela vison,* and otter *Lontra* and *Enhydra* species) are adapted to forested habitats, where spatio-temporal variation is greater than grasslands or savannahs (Eisenberg 1981). Characteristics of their environment likely relate to life history adaptations that promote fitness for that environment. For example, Oftedal (1984) argued that forest-dependent species live in an environment that is nutritionally limiting relative to open environments, and therefore carnivore species have evolved later sexual maturity as part of slower growth. Similarly, specific life history adaptations will correlate with management considerations. For example, mustelid populations are predicted to support trapping of juveniles but not adults (Ferguson and Larivière 2002).

Recent results suggest that many populations of carnivore species, including mustelids, are over-exploited by humans and living in habitats considerably altered by human activities (Ruggiero et al. 1994, Fuller and Kittredge 1996, Mech 1996). The result is the extinction of subspecies (Kucera et al. 1995) and the isolation of populations (e.g., Snyder and Bissonette 1987, Gibilisco 1994, Zielinski et al. 2001). In contrast, some populations of North American carnivores, including mustelids, can withstand high trapping pressure (Hodgman et al. 1994, Oehler and Litvaitis 1996, Larivière et al. 2000). For fisheries, evidence suggests a relationship between life histories and tolerance to exploitation (Trippel 1995, Jennings et al. 1998). The role of life histories in determining conservation methods, such as done for birds (Saether et al. 1996) and for carnivores (Ferguson and Larivière 2002), remains largely unexplored for mustelids.

Our goal is to provide a method for predicting vulnerability to overexploitation of harvested populations based on particular life histories (e.g., Sutherland and Reynolds 1998). For example, species that invest less maternal energy in progeny may tolerate the trapping of juveniles without significantly affecting population density. Conversely, these same species may not abide trapping of adults, which are more valuable to maintaining successful population demography. Also, species with life history adaptations to unpredictable climatic conditions or a heterogeneous distribution of energy across time and space may require the conservation of these environmental conditions to provide the demographic advantages over competitors that have life histories adapted to predictable environments.

We describe differences in life-history strategies between mustelids and other North American carnivores to explore whether mustelids warrant special conservation strategies. We used the comparative approach to control for non-independence of species data (Harvey and Pagel 1991). Previously, Ferguson and Larivière (2002) grouped some mustelid species with bears *(Ursus)* into a group called “bet-hedgers” that, relative to other carnivores, lived in unpredictable low energy environments and are characterized by low maternal investment in reproduction while extending the chronology of reproductive events. Specific predictions include later age at sexual maturity, longer interbirth interval, greater longevity, shorter gestation length, smaller neonate mass, and shorter duration of weaning relative to non-mustelid carnivores. As well, we predict that relative to other carnivores, mustelids inhabit highly seasonal environments, live at lower population densities, have larger home ranges, have longer estrus periods, have a greater likelihood of using multi-male mating systems (versus monogamy or polygyny), and have greater sexual dimorphism.

2. METHODS

2.1 Phylogeny and Data

Extant members of Mustelidae are diagnosed as a monophyletic group on the basis of the carnassial notch on the upper fourth premolar, the loss of the upper second molar, as well as enlarged scent glands (Martin 1989, Wozencraft 1989, Bryant et al. 1993). We used the phylogenetic tree proposed by Bininda-Emonds et al. (1999) and the taxonomy of Wozencraft (1993), except that we considered skunks as a separate family, Mephitidae (Dragoo and Honeycutt 1997, see Ferguson and Larivière 2002). The data consisted of 6 families, 21 genera, and 38 species of North American terrestrial carnivores of which 10 were mustelids. We did not use information for marine carnivores (i.e., pinnipeds and sea otter *Enhydra lutis*), as this group possesses unique life-history traits distinct from terrestrial carnivores (Ferguson et al. 1996).

We obtained data on life-history and behavioral traits from published sources (e.g., *Mammalian Species* articles). See Ferguson and Larivière (2002) for the complete data set. Where more than one value was available, we used the mean and if a range was reported we used the midpoint. All data were $\log_{10}$ transformed before analysis to meet assumptions of normality (Harvey and Pagel 1991). Gestation length refers to the time from implantation to parturition and, therefore, does not include the period of delayed implantation.

We estimated productivity and variation in productivity within the historical geographic range (Novak et al. 1987, Nowak 1991) of each carnivore species in North America (Ferguson et al. 1996). We estimated site-specific actual evapotranspiration (mm m-2 y-1) for a set (n = 112) of weather stations located across North America that provided greater than 30 years of continuous weather information (Zeveloff and Boyce 1988). Tables and equations of Thornthwaite and Mather (1957) and climate data were used to calculate energy and seasonality as the total and the coefficient of variation (CV) of monthly (n = 12) values of actual evapotranspiration respectively. Actual evapotranspiration represents the amount of rainfall returned to the atmosphere and is calculated from a site's latitude, soil and vegetation type, and mean monthly temperature and rainfall. Actual evapotranspiration generally increases with a site's solar input, precipitation, and soil capacity and is highly correlated with primary productivity (Rosenzweig 1968). Hence, actual evapotranspiration is used as a productivity surrogate in a variety of studies (e.g., Currie 1991, Ferguson and McLoughlin 2000, Kaspari et al. 2000). We used Lieth's (1976) algorithm to correlate actual evapotranspiration to total net primary productivity. Large primary productivity values indicate greater energy within a species' geographic range. Similarly, large CV values indicate large seasonality within the range of a species.

Mating systems are often coded as categorical data, although the information can also be interpreted as a continuous variable (Garland et al. 1993). We grouped mating systems as polygynous (one male mating >3 females in one area over a relatively short breeding season), multi-male mating (one male mating 1–3 females over a large area and over a relatively long breeding season), and monogamous (one male generally breeds with one female) using the following three category-ordered variables: 3 = polygyny, 2 = multi-male, 1 = monogamy. Multi-male mating occurs in populations where males increase their range during the mating season to encompass a number of female ranges and females are often mated by a number of males (Schenk and Kovacs 1995, Schenk et al. 1999). Mating system was compared using analysis of covariance with female body mass as the covariate. Although mating system was treated as a continuous variable, only one species *(Mephitis mephitis)* was considered polygynous and, therefore, the results are comparable to treating the data as categorical.

2.2 Statistical Analyses

We tested whether mustelids have predictable differences in life-history and behavioral traits compared to other carnivores (see introduction). Phylogenetic corrections are necessary when variation in the observed data set results from phylogenetic structure, creating non-independence of data points (Harvey and Pagel 1991). We tested for the hierarchical pattern of variation in life-history and behavioral traits using nested analysis of variance at three taxonomic levels (species, genus, family). Nested ANOVA provides a suggestion of the taxonomic level that should be used for analysis (Harvey and Pagel 1991). We assume that most variation occurring at the family level indicates the need for phylogenetic correction methods. Conversely, if most variation occurred at the species level then phylogenetic corrections may not be necessary. This selection criterion is somewhat arbitrary and therefore we provide both phylogenetically corrected and conventional statistical results.

We used Monte Carlo algorithms to incorporate phylogenetic structure (i.e., phylogenetic tree) from 38 species (2 polytomies) to estimate statistical parameters for phylogenetic analysis of covariance (ANCOVA) (Garland et al. 1993). Initial limits corresponding to life-history and behavioral traits were obtained from the average of all species values. We performed simulations according to the gradual model of speciation that assumes variance changes are proportional to branch lengths. For each simulated dataset (n = 1,000), we calculated phylogenetically corrected estimates of ANCOVA parameters using general linear models. Conventional ANCOVA statistics were calculated from the observed sample data and compared to the distribution of simulated test statistics. ANCOVA adjusts for differences associated with body mass between groups and enables the assessment of differences in traits due to groups alone. Least-squared means of adjusted trait values represent the predicted mean value for traits after regressing traits on body mass for each group. The ANCOVA model used Type III sum of squares to determine the statistical difference between the least-squared (adjusted) means associated with each group. The phylogenetically corrected critical value of differences due to group (mustelids and others) was set at alpha = 0.10 from the 90th percentile of the simulated distribution. Significant differences are reported in least-squared means that control for body size variation.

3. RESULTS

We found considerable differences among traits as to what phylogenetic level most variation occurred (Table 1.1). Most variation in species traits was attributable to differences within family (median = 42.3, range = 0.9–88.8) and within species (median = 53.0, range = 0.0–94.8), but relatively little variance was explained at the level of genera (median = 9.5, range = 2.0–37.1). The greatest variance in traits occurred at the family level relative to genera or species level for mating system, weaning duration, gestation length, neonate mass, age at maturity, litter size, and interbirth interval. These results indicate that phylogenetic correction methods are necessary for statistical comparisons of these life-history traits. Once we corrected for phylogeny, only gestation length differed between mustelids and other carnivores ($P = 0.09$; Table 1.2). Mustelids had shorter gestation length (Fig. 1.1) relative to other terrestrial carnivores. Although not significant, the general trend was for mustelids to have smaller neonates, smaller litter size, later age at maturity, longer interbirth interval, and longer life relative to other carnivores (Table 1.2).

All mustelids have multi-male mating systems. In comparison, other terrestrial carnivores adopt monogamous (32%), multi-male (64%) and polygynous (4%) mating systems. Despite these apparent differences, mating systems did not differ between the two groups once we corrected for phylogenetic effects (Table 1.2).

Table 1.1. Comparison of relative percent of variance attributable at the species- (n = 38), genera- (n = 21) and family- (n = 6) level for 8 life-history and 7 behavior traits for species of North American carnivores using a nested analysis of variance for each variable. Bold indicates the level with greatest percent of variation explained.

Life-history and Behavior Traits	Percent of Total Variance Family	Genera	Species
Mating system	**88.8**	11.2	0.0
Weaning duration	**64.5**	2.0	33.5
Gestation length	**61.3**	11.6	27.1
Neonate mass	**52.2**	37.1	10.6
Age at maturity	**51.2**	5.3	43.5
Litter size	**48.1**	32.3	19.5
Interbirth interval	**47.9**	6.0	46.1
Longevity	42.3	4.7	**53.0**
Male home range	16.3	19.9	**63.8**
Seasonality	29.8	2.4	**68.2**
Duration of estrus	7.9	22.5	**69.6**
Female home range	3.8	25.8	**70.4**
Sexual dimorphism	21.3	4.4	**74.3**
Population density	1.0	9.5	**89.5**
Primary productivity	0.9	4.3	**94.8**

Longevity, male home range size, seasonality, duration of estrus, female home range size, sexual dimorphism, population density, and energy (primary productivity) had the greatest variance attributable to the species level (Table 1.1). This pattern of variation suggests that phylogenetic correction may not be necessary for these variables. Using conventional ANCOVA statistics, we found that mustelids differed from other carnivores in sexual dimorphism, population density, male home range size, and length of estrus. Relative to other carnivores, mustelids had greater sexual dimorphism ($P = 0.05$; Fig. 1.2), lower population density ($P = 0.09$; Fig. 1.3), larger male home range size ($P = 0.04$; Fig. 1.4), and longer estrus periods ($P = 0.02$; Fig. 1.5). A significant interaction effect occurred in sexual dimorphism between mustelids and other carnivores indicating a difference in slope: larger mustelids were less dimorphic, whereas larger carnivores were more dimorphic (Fig. 1.2). Comparing environmental variables, mustelids lived in more seasonal environments ($P = 0.01$; Fig. 1.6) but energy (primary productivity) in these environments did not differ from other terrestrial carnivores ($P = 0.33$; Table 1.2).

Figure 1.1. Relationship between gestation length (days) and female body mass (g) for mustelids (n = 10) and other terrestrial carnivores in North America (n = 28)

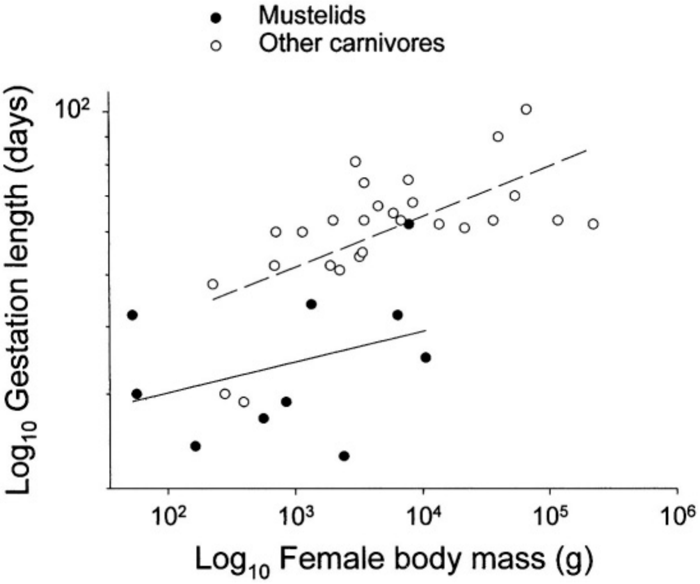

Figure 1.2. Relationship between sexual dimorphism (male/female mass) and female body mass (g) for mustelids (n = 11) and other terrestrial carnivores in North America (n = 27)

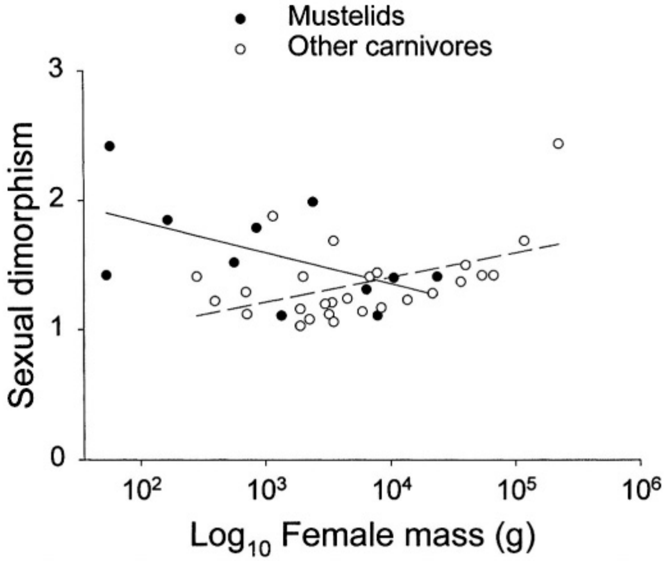

Table 1.2. Difference between mustelids ($n = 10$) and other terrestrial North American carnivores ($n = 28$) for 8 life-history and 7 behavior traits using analysis of covariance tests. The covariate is female body mass except in the case of male home range size when male body mass is the covariate. Models of evolutionary change were no phylogenetic change (standard ANCOVA) or gradual evolutionary change (proportional to branch lengths). Bold represents significant differences using conventional or phylogenetic tests based on results from Table 1.

Life-history and behavior traits	Conventional ANCOVA				Least-square means		Phylogenetic correction	
	n	Observed *F*	Critical *F*	*P*	Mustelids	Other	Critical *F*	*P*
Weaning duration	33	0.11	4.16	0.74[a]	70.80	76.70	22.8	0.88
Gestation length	38	20.50	4.10	<0.01	37.90	57.80	23.3	**0.09**
Neonate mass	34	7.68	4.15	0.01	47.00	86.50	37.2	0.49
Age at maturity	37	0.41	4.11	0.53	542.00	481.00	36.8	0.85
Litter size	38	0.27	4.10	0.61	3.20	3.50	23.7	0.71
Interbirth interval	37	1.69	4.11	0.20	430.00	379.00	26.4	0.59
Longevity	36	0.06	4.12	0.81	4,656.00	4,550.00	36.2	0.99
Male home range	31	4.72	4.17	**0.04**	28.90	8.80	28.3	0.32
Seasonality	38	8.64	4.10	**0.01**	1.14	0.87	22.7	0.20
Duration of estrus	23	6.49	4.34	**0.02**	19.30	5.10	56.3	0.35
Female home range	31	2.59	4.17	0.12	21.30	6.80	29.9	0.44
Sexual dimorphism	38	4.18	4.10	**0.05**[a]	1.58	1.32	23.8	0.33
Population density	30	3.02	4.18	**0.09**	0.31	1.07	26.0	0.46
Primary productivity	38	0.97	4.10	0.33	987.00	1,082.00	27.3	0.71
Mating system	38	2.02	4.10	0.16[a]	1.99	1.72	25.3	0.78

[a] Slopes differ significantly between groups.