

Chapter 1

IS MUSTELID LIFE HISTORY DIFFERENT?

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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 ($\text{mm m}^{-2} \text{y}^{-1}$) for a set ($n = 112$) of weather stations located across North America that provided greater than 30 years of continuous weather information (Zevuloff 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 ($n = 28$)

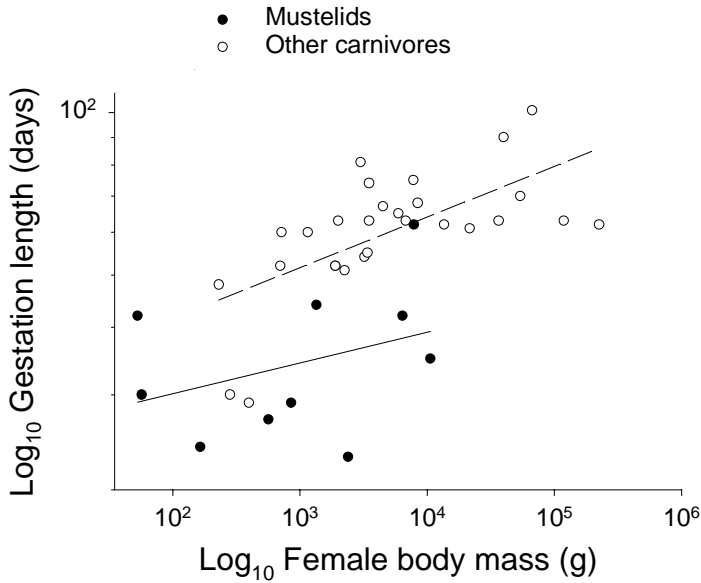


Figure 1.2. Relationship between sexual dimorphism (male/female mass) and female body mass (g) for mustelids ($n = 11$) and other terrestrial carnivores in North America ($n = 27$)

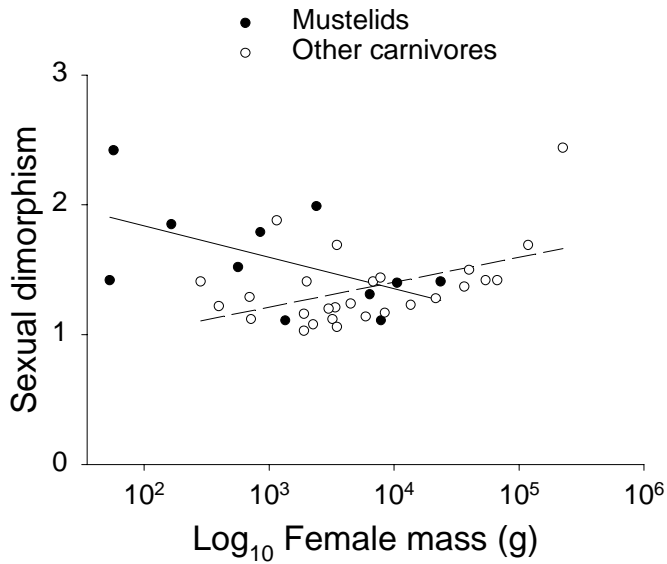


Table 1.2. Difference between mustelids ($n = 10$) and other terrestrial North American carnivores ($n = 28$) for 8 life-history and 7 behavior traits using analysis of covariance tests. The covariate is female body mass except in the case of male home range size when male body mass is the covariate. 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	n	Conventional ANCOVA		Least-square means		Phylogenetic correction		
		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

^aSlopes differ significantly between groups.

Figure 1.3. Relationship between population density (individuals/km²) and female body mass (g) for mustelids ($n = 10$) and other terrestrial carnivores in North America ($n = 20$).

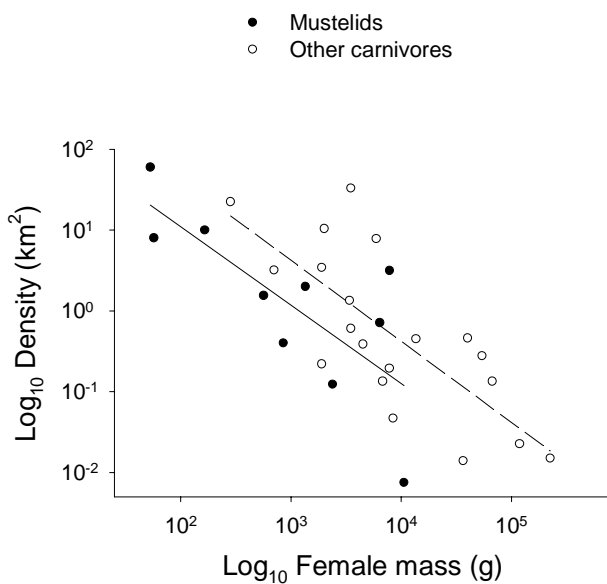


Figure 1.4. Relationship between male home range size (km²) and male body mass (g) for mustelids ($n = 10$) and other terrestrial carnivores in North America ($n = 21$).

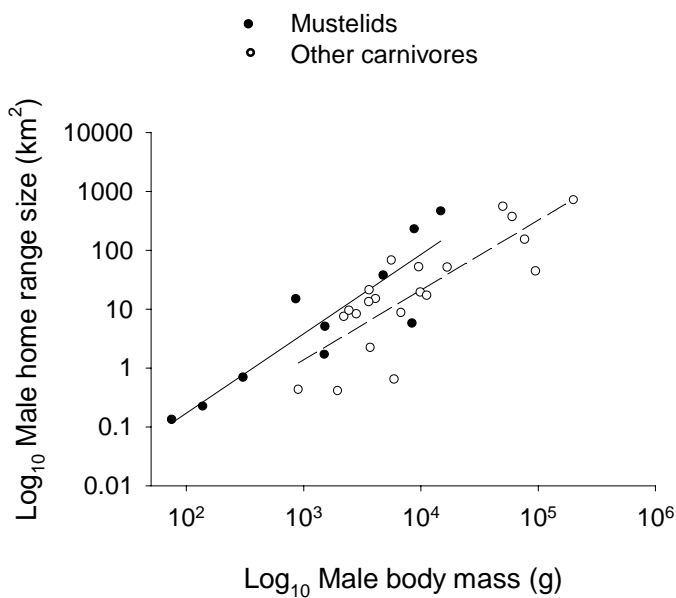


Figure 1.5. Relationship between duration of estrus (days) and female body mass (g) for mustelids ($n = 6$) and other terrestrial carnivores in North America ($n = 17$).

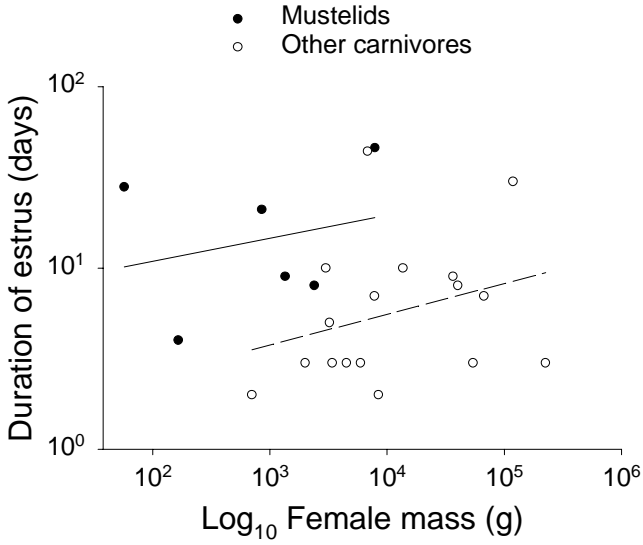
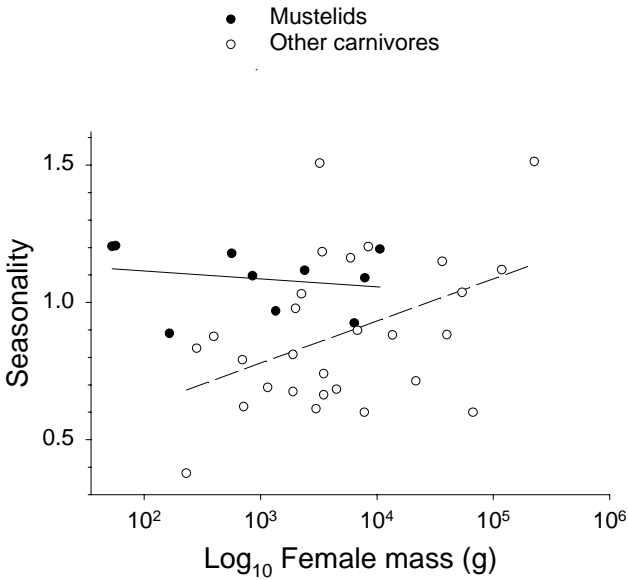


Figure 1.6. Relationship between seasonality (coefficient of variation) and female body mass (g) for mustelids ($n = 10$) and other terrestrial carnivores in North America ($n = 28$).



4. DISCUSSION

Previous research has found that mustelid life history is relatively different from many other carnivore groups in social system (Johnson et al. 2000), home range size (Lindstedt et al. 1986, Buskirk and McDonald 1989), delayed implantation (Sandell 1990, Ferguson et al. 1996), induced ovulation (Amstislavsky and Ternovskaya 2000, Larivière and Ferguson 2003), sexual dimorphism (Erlinge 1979), and baculum size (Larivière and Ferguson 2002). Mustelids did not exhibit the K-selected life history strategies of high longevity, slow growth, and low fecundity, but rather were characterized by the life-history adaptations referred to as bet-hedgers (Ferguson and Larivière 2002). Our results provide the first statistical evidence using the comparative approach to identify a suite of interacting life history and behavioral traits of mustelids that differ from other terrestrial carnivores. These interacting traits may have relevance to management and conservation by suggesting that mustelids require different conservation strategies.

Mustelids inhabit highly seasonal environments, have larger home ranges, and lower population densities compared to other terrestrial carnivores. Low densities imply small populations (Gaston 1996), and small populations are predisposed to stochastic and genetic changes that lead to extinction (Gilpin and Soulé 1986). For example, wolverines (*Gulo gulo*) occur at extremely low densities (0.006–0.02/km², Pasitschniak-Arts and Larivière 1995) and range widely, which predisposes them to impacts from humans (Finch 1992). Furthermore, low densities and large home ranges suggest that mustelids require larger areas for their conservation, and that they may be more sensitive to trapping than other carnivores (Kyle and Strobeck 2002). Large home ranges also suggest that mustelids are more likely to be affected by human activities (Wilson et al. 2000). Already, some mustelid species have undergone distributional losses (reviewed by Ruggiero et al. 1994) that have been attributed to humans. Undoubtedly, maintenance or preservation of large patches of suitable habitat will remain one of the priorities for conservation of mustelids, especially relatively large-bodied species that inhabit boreal forests (e.g., *Martes*; Helldin 2000, Potvin et al. 2000, Rondinini and Boitani 2002).

Mustelids likely evolved in temperate areas (King 1986) characterized by high seasonality. Adaptations for life in seasonal high-latitude environments that are more unpredictable (Ferguson and Messier 1996) include the evolution of delayed implantation in mustelids (Sandell 1980, Ferguson et al. 1996). Life history comparisons suggest that mustelids have generally evolved a “bet-hedging” life-history strategy that maximizes reproduction in unpredictable seasonal environments occurring at high latitude/altitude. Previously, we iden-

tified a group called “bet-hedgers” that consisted of ursids (black *Ursus americanus*, brown *U. arctos*, and polar bears *U. maritimus*) and forest-dwelling mustelids (martens *Martes americana*, fishers *M. pennanti*, and wolverines) that were characterized by short gestation, small neonate mass, large litters, late maturation and long life (Ferguson and Larivière 2002). If juvenile survival responds more strongly to environmental conditions than adult survival, then the best option for a parent is to keep its own survival probability high and reproductive effort low (Both et al. 1999, Lindstrom 1999). The pattern of low maternal investment in offspring for mustelids relative to other carnivores was indicated by short gestation length and small neonates, although the latter was not significant with phylogenetic corrections. The unpredictability of high-latitude seasonal environments is intensified by the time delay between reproductive decisions made by the parents and the environmental conditions that the offspring face at birth.

Environmental unpredictability is a key component of mustelid environments, and one component that managers often fail to address. Most forest animals, including many mustelids, are adapted to the natural disturbance regimes of fires, windfalls, and disease (Ruggiero et al. 1994). For example, martens, fishers and in southern parts of their range, wolverines are generally thought to require large areas of old-growth forest (Hornocker and Hash 1981, Powell 1993, Buskirk and Powell 1994) rather than the mixed landscapes of different-aged stands created by disturbance such as fire or logging. Thus, forest management guidelines (e.g., Watt et al. 1996) specify the legal requirement of maintaining old growth forest for mustelids. Nevertheless, studies have found mustelids surviving and reproducing in younger forests (e.g., Banci 1987, Arthur and Krohn 1991, Chapin et al. 1997, Potvin et al. 2000), suggesting that mustelid population dynamics are adapted to highly dynamic environments, such as occurs with fire-cycles in boreal forests or spruce budworm (*Choristoneura fumiferana*) cycles in Acadian forests (Attiwill 1994). In fact, mustelids may depend on unpredictability to ‘out-compete’ more generalist carnivores, which are characterized by greater fecundity and higher recruitment (Ferguson and Larivière 2002).

The American marten provides a well-studied example of mustelid life history. The marten was historically distributed throughout the northern boreal, mixed Acadian forests, and northeastern Appalachian forests of North America (Gibilisco 1994). Martens have low reproductive potential and hence require protection from loss of habitat (Snyder 1986, Forsey et al. 1995). Relative to other mammals, martens display a prolonged time to sexual maturity, litter size is as expected on the basis of body size, interbirth interval may be shorter than allometric predictions, yearly reproductive output of pregnant female martens

is low, and longevity is high (Buskirk and Ruggiero 1994). Trapping has contributed to the loss of martens in some areas, including the north-central states and eastern Canada (Buskirk and Ruggiero 1994). A successful method of restoring mustelid populations in Minnesota, U.S.A., was to close the trapping season to conserve martens and fishers (Mech 1996). In addition to trapping, marten populations can fluctuate in response to resource conditions that result from cyclic changes in prey density and loss of physical structure of the forest, such as timber harvesting (Fryxell et al. 1999, Helldin 2000).

The life histories of mustelids have management and conservation implications in an increasingly fragmented habitat because of anthropogenic causes. Mustelids exhibit multi-male mating systems, long estrus periods, delayed implantation, induced ovulation, and large sexual size dimorphism relative to other terrestrial carnivores. As well, mustelids live in seasonal environments characterized by snowfall in winter and demanding energetic conditions (Wilbert et al. 2000), and they occur at low densities and range over large areas. These reproductive and behavioral traits relate to a multi-male mating system adapted to the environmental conditions that make it difficult for male and female mustelids to get together. The multi-male mating system promotes sexual selection (Rowe and Arnqvist 2002) and increases genetic variation (Petrie et al. 1998). A conservation consequence of the multi-male mating system and associated genetic variation may be increased local population extinctions. Thus, there is a need to retain gene flow via linked populations among fragmented habitat to sustain populations that are sensitive to inbreeding (Schwartz et al. 2002).

Increasing concern for the conservation status of many mustelids (Fuller and Kittredge 1996) makes assessments of their vulnerability to over-trapping and habitat loss more important (Ruggiero et al. 1994). Our analyses suggest that mustelids show life history adaptations to high latitude environments characterized by variability. The conservation outcome of these adaptations includes the need to maintain genetic linkages among populations and the need to maintain environmental variability across time and space. Environmental variability preserves the advantage afforded by mustelid life histories over their carnivore competitors. The approach of comparing life histories should have general applicability to other taxa, as conservation biologists search for general resource and spatial requirements that can be used to identify minimum conditions necessary for long-term population persistence (Smallwood 1999). Forested landscapes are rapidly being converted to intensive human uses (Turner 1987, Chapin et al. 1998) and traditional forest management results in fragmented habitats, thereby leading to loss of biological diversity (Wallin et al. 1994, Hargis et al. 1999). We argue that a broader understanding

of the relationship between life-history patterns and population processes may facilitate the development of general principles to help managers understand the impact of forest disturbance and trapping on mustelids.

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