

Does seasonality explain the evolution and maintenance of delayed implantation in the family Mustelidae (Mammalia: Carnivora)?

Steven H. Ferguson, Jeff W. Higdón and Serge Larivière

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Understanding the evolutionary pressures that may have led to the development and retention of delayed implantation in mammals remains an enigmatic puzzle for evolutionary ecologists. Recent studies suggest a strong role of environmental conditions but other attributes of species, notably body size and life history traits, may obscure primary mechanisms. Following the recommendation of Lindénfors et al., we examined environmental correlates related to the evolution of delayed implantation and its subsequent maintenance or loss in the family Mustelidae (Mammalia: Carnivora). We focused on the Mustelidae because evolution and subsequent loss of delayed implantation occurred most commonly within this group. Data on 34 species of mustelids from around the world suggest that delayed implantation may have evolved when optimal times for mating and birthing are separated by more than a gestation period, characteristic of environments with long winters that reduce the opportunities to find mates. Environmental characteristics (seasonality, temperature, snow, latitude, and primary productivity) were highly intercorrelated but seasonality was the best predictor of the evolution or loss of delayed implantation via population traits. Here, structural equations on phylogenetic independent contrasts revealed that high seasonality was correlated with low population density and large individual home range size, which in turn was correlated with presence/absence of delayed implantation. We argue that the evolution of delayed implantation provides the reproductive means to mate during the season (summer) with the greatest prospects for females to ‘choose’ mates when living in high-latitude seasonal environments that generally reduce these opportunities (i.e. low population density and large ranges). Body mass of female mustelids did not differ between species with and without delayed implantation, refuting the hypothesis that loss of delayed implantation is an evolutionary by-product of evolving to smaller size. We conclude that understanding the environmental selection pressures responsible for the evolution of life history traits related to density and spacing behaviour allows for a more complete picture of the evolution and subsequent loss of delayed implantation.

S. H. Ferguson, Fisheries and Oceans, 501 University Crescent, Winnipeg, MB, Canada, R3T 2N6 (fergusonsh@dfö-mpo.gc.ca). – J. W. Higdón, Faculty of Environment, Earth and Resources, Univ. of Manitoba, 501 University Crescent, Winnipeg, MB, Canada, R3T 2N6. – S. Larivière, Cree Hunters and Trappers Income Security Board, 2700 Boulevard Laurier, Sainte-Foy, QC, Canada, G1V 4K5.

The origin and evolution of delayed implantation is a puzzling characteristic of mammalian reproduction, and many hypotheses have been advanced to explain the adaptive value of such phenomena. One such hypothesis is that delayed implantation is strongly linked to fluctuation of environmental conditions caused by

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seasonality. Seasonality, defined as the annual variation in environmental conditions and primary productivity, is an important evolutionary pressure affecting the life history and behaviour of mammals (Rosenzweig 1968, Boyce 1979, Andersson 1994). Seasonality also affects reproduction because mammals living in high latitude seasonal environments must give birth and raise young during the short summer season when conditions are favourable. In northern latitudes where the favourable summer season is often brief, early parturition allows for maximum offspring growth by maximising the time of positive energy balance. Thus, parturition of most large-bodied mammals (>100 g) living at high latitudes occurs in spring. In mammalian species with relatively fixed gestation length, time of mating determines time of parturition. In contrast, species with delayed implantation may uncouple mating and parturition (Aitken 1974, Sandell 1990, Ferguson et al. 1996, Thom et al. 2004) and thus be able to shift their mating season away from the snow season to a time when males are more mobile and can better find receptive females. Evolutionary pressures related to seasonality have been directly linked to mammalian reproduction and the presence of reproductive traits (Beck et al. 2003, Larivière and Ferguson 2003, McNamara et al. 2004, Ferguson and Larivière 2004a). Environmental selection pressures are thus likely also responsible for both the evolution of changes in body size and subsequent loss of delayed implantation among carnivores.

In this respect, delayed implantation may enhance mating opportunities for males and females thereby facilitating mate choice. By mating during the summer season, females may encounter more mates, and can either assess male quality phenotypically, or use pre-copulatory and postcopulatory mechanisms to confer mate selection. The hypothesis that delayed implantation permits the uncoupling of mating and parturition events (Sandell 1990), allowing both to occur at a time of optimal environmental conditions, was supported using tests on data from North American carnivores (Ferguson et al. 1996). However, an alternative explanation postulates that delayed implantation is unrelated to seasonality but rather its loss in mammalian carnivores is related to the evolution of smaller body size (Lindenfors et al. 2003).

Here we test the hypothesis that delayed implantation is more likely to evolve in mammalian carnivores when the optimal times for mating and birthing are separated by more than a gestation period, and that this is likely to happen in environments with long winters (i.e. greater seasonality). Our primary prediction is that delayed implantation evolved in mammalian species living in high latitude environments characterized by greater seasonality, low primary productivity, greater snowfall, and low temperatures relative to environments lived in by carnivore species without delayed implantation.

Lindenfors et al. (2003) argued that delayed implantation has a monophyletic origin, and that because most losses and possible gains of delayed implantation occurred within the Mustelidae, evolutionary tests of hypotheses should be applied to this family. To test our predictions, we used data on mustelid carnivores with variable body mass and life histories (Ferguson and Larivière 2002, 2004b). We used comparative methods because species may not represent independent data points (Harvey and Pagel 1991, Garland et al. 1993). Additionally, we empirically tested the hypotheses put forth by Lindenfors et al. (2003) that body size can explain the loss of delayed implantation in the Mustelidae (Mammalia, Carnivora) of the world. We test multiple hypotheses about the evolution of delayed implantation using an information-theoretic approach that compares Akaike's information criterion (AIC), thus providing a quantitative method to choose a final model that has both simplicity and high predictive power (Burnham and Anderson 2002).

Material and methods

Data sources

In the mammalian Carnivora, there are 12 recognized families (Wozencraft 1993, Drago and Honeycutt 1997): Canidae, Felidae, Herpestidae, Hyaenidae, Mephitidae, Mustelidae, Odobenidae, Otariidae, Phocidae, Procyonidae, Ursidae, Viverridae. Among those, delayed implantation is documented in the Ursidae, Mustelidae, Mephitidae, Odobenidae, Otariidae, and Phocidae (Ferguson et al. 1996). We used the portion of the carnivore phylogenetic tree proposed by Bininda-Emonds et al. (1999) that consisted of 43 species of world mustelids, 34 of which we had information on the presence/absence of delayed implantation, and the taxonomy of Wozencraft (1993). We obtained published data on species' life history and behavioural traits (e.g. mammalian species articles; see Ferguson and Larivière 2004a), which is available upon request from the authors. Data on density and home range of species were obtained from summary literature (Bininda-Emonds 1998, Kelt and Van Vuren 2001, Ferguson and Larivière 2002, 2004a). For species values, we used means of population estimates from different areas of the world. Species with a short delayed implantation (<2 week; *Mustela vison*, *Mephitis mephitis*, *Conepatus* sp.; versus >4 months for all other mustelids) were considered to not have delayed implantation (Renfree and Shaw 2000), as a 2-week delay is not long enough to provide advantage in seasonal environments.

Longitude and latitude of the midpoint of each species historical distribution was obtained using maps from mammalian species accounts and world maps (Ferguson and Larivière 2004a). Environmental data for species

were taken from the latitude/longitude at the centre point of the historical distribution of each species. When a species occurred on more than one continent, we used the midpoint of the continent containing the larger range distribution. Environmental variables included latitude (absolute value), seasonality, primary productivity, snow accumulation, and temperature. Seasonality was calculated using a water budget analysis (Thorntwaite 1948) of data from 13 332 weather stations distributed over the globe and then spatially interpolated to a regular grid of 1° by 1° latitude–longitude intervals (Wilmott et al. 1985). Seasonality was calculated as the coefficient of variation of monthly ($n=12$) values of actual evapotranspiration ($\text{mm} \times \text{m}^{-2}$, Ferguson 2002). Actual evapotranspiration generally increases with solar input, precipitation, and soil water holding capacity and is highly correlated with primary productivity (Currie 1991, Ferguson and McLoughlin 2000, Kaspari et al. 2000). Leith's (1976) algorithm was used to convert actual evapotranspiration to total net primary productivity ($\text{g m}^{-2} \text{y}^{-1}$). Larger primary productivity values and larger coefficients of variation indicated greater energy and seasonality within a species' geographic range, respectively. We used the absolute values for latitude to compare similar latitude locations in the northern (positive; $n=90$) and southern (negative; $n=30$) hemispheres. After ensuring positive values for all traits (snow+0.5, temperature+300) all variables were \log_{10} transformed before analyses.

Comparative analyses

Comparative analyses may not reflect species variability as well as traditional non-phylogenetic methods. Thus, we used a test for phylogenetic signal in comparative data that assumes Brownian motion evolution (Blomberg et al. 2003) using the Phenotypic Diversity Analysis Program (PDAP version 6) package (Garland et al. 1993, 1999, 2001). The program fits the tip data (e.g. body mass) to the tree according to the variance of standardized independent contrasts. To control for body size, we computed size-corrected values as described by Blomberg et al. (2003) by log-transforming trait values, computing standardized phylogenetically independent contrasts for both traits, computing least-squares linear regression through the origin for the contrasts, and using the computed allometric exponent (b) to size correct according to: original trait (not contrasts) = $\log(\text{trait}/(\text{size}^b))$. The variance (mean square error) was compared with the distribution of values from 1000 random permutations across the tips of the tree.

First, we used linear regression of independent contrasts to test whether population density was related to home range size while controlling for female body mass. We calculated standardized independent contrasts by

dividing the unstandardized contrast by the standard deviation using Felsenstein's (1985) method (PDTREE module of PDAP; Garland et al. 2001). Many traits coded as two (e.g. presence/absence of delayed implantation) categories can be treated as a quantitative variable and analyzed as any other continuous variable using independent contrasts (Purvis and Rambaut 1995, Garland et al. 2005). Second, we used analysis of covariance to test for size-related explanation of the evolution of delayed implantation in mustelids (Lindfors et al. 2003). We used Monte Carlo simulations to estimate parameters for analyses of covariance that incorporate phylogenetic structure by simulating character evolution (Garland et al. 1993).

Cause and effect models

Last, we tested for relationships among variables using a multiple hypothesis framework (Anderson et al. 2000, McIntire 2004), while controlling for the effects of phylogeny. Many important ecological and evolutionary processes are influenced by multiple interacting factors (Quinn and Dunham 1983) that are best analysed using path analysis and structural equations (Petraitis et al. 1996, McIntire 2004). An a priori path model approach was used to describe formal hypotheses testing in the presentation of contrasting path models. Hence, the causal models are separate from the data used to estimate strength of paths in the model. Here, we used independent contrasts to control for phylogeny allowing for exploration for differences in traits due to environment and behaviour alone (i.e. variation in phylogeny has been statistically removed from the analysis). The multiple hypotheses used in this study were generated based on a mechanistic understanding of relationships between variables (Fig. 1). In an a priori model approach, each model must be justified based on logic and prior ecological knowledge.

The adjusted trait values were used in model comparisons with the covariance analysis of linear structural equations (CALIS procedure; SAS 1999), which estimates parameters and tests the appropriateness of linear structural equation models using covariance structure analysis. Structural equations express relations among several variables that can be either directly observed variables (manifest variables) or unobserved hypothetical variables (latent variables). For maximum-likelihood estimation, the random variables are assumed to have an approximately multivariate normal distribution. We used a set of structural equations (LINEQS statements) to describe the models with the Levenberg-Marquardt optimization technique that usually is the most reliable (i.e. with poor initial values). The procedure creates an output data set that describes the model and estimates parameters. No intercepts were specified in the linear

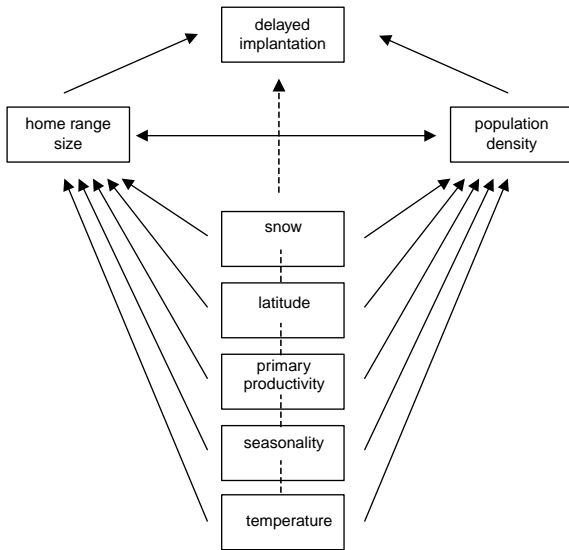


Fig. 1. Hypothesized path models predicting the influence of environment on population density, home range size, and delayed implantation for 34 mammalian mustelid species. Environmental characteristics are the assumed explanatory causal pattern and no latent factors are included in the analyses.

equations (i.e. the regressions runs through zero) as required with the use of phylogenetic independent contrasts (Garland et al. 1999).

Some general model information, univariate statistics, and the analyzed covariance matrix indicated model appropriateness. The optimization parameters include the goodness-of-fit statistics, which indicate the appropriateness of the linear structural equation model for the given data set (covariance matrix). Chi-square measure is the likelihood ratio test statistic for the null hypothesis that the predicted matrix has specified model fit against the alternative that the model is not well fit. Thus the

probability denotes the likelihood under the null hypothesis and a larger p indicates the better model (McArdle and Hamagami 2003). We assessed model fit using Akaike's information criterion (AIC), which is preferred for small sample sizes (Bozdogan 1987). The model that yields the smallest value of AIC is considered most appropriate and provides another criterion for choosing the best number of parameters to include in a model, particularly since we used maximum-likelihood estimation.

All 24 models were tested for absolute fit as well as relative fit by comparing goodness-of-fit statistics using modified Akaike's information criterion for small samples (AIC_c ; Burnham and Anderson 2002). Akaike differences (Δ_i) and normalized Akaike weights were calculated (w_i). In general, where $0 < \Delta_i < 2.0$, the models were considered to have substantial support (McIntire 2004, Vucetich and Peterson 2004).

Results

For the comparative data from 43 mustelid species, a significant phylogenetic signal occurred in the variation of six of the nine traits (Table 1). Latitude, seasonality, and primary productivity were the only trait values that did not have a significant proportion of variation explained by phylogeny. We used phylogenetically corrected analyses for all traits in general linear and structural equation models.

All four measures of environment (latitude, seasonality, snow, and temperature) were significantly correlated (11 tests) using conventional or phylogenetic analyses ($r^2 > 0.23$, $p < 0.01$) with the exception of latitude and snow ($r = -0.087$, $p = 0.58$) and primary productivity and latitude ($r = -0.334$, $p = 0.18$). Using regression analysis of independent contrasts (controlling

Table 1. Statistical analyses of mustelid species' traits for phylogenetic signal.

Trait	n^1	Slope ²	MSE ³	K^4	p^5
Female mass	43	NA	0.063303	0.188	0.001
Delayed implantation	34	-0.0121	0.006186	0.472	0.048
Density	19	-0.7984	0.115491	0.464	0.010
Home range	25	1.50645	0.064027	0.407	0.041
Temperature	43	+0.00780	0.0052074	0.400	0.003
Snow	43	-0.06809	0.4917085	0.413	0.037
Latitude	43	-0.05221	0.2777402	1.710	0.51
Seasonality	43	-0.38541	0.1478457	1.125	0.42
Primary productivity	43	0.337227	0.1306108	1.154	0.73

¹ n = sample size is the number of mustelid species for which trait values were obtained from literature and geographic analyses

²Slope is the allometric exponent calculated using least-squares linear regression through the origin for standardized phylogenetically independent contrasts of trait vs female body mass (male body mass is used for the analysis of the female body mass trait)

³MSE = mean squared error corrected for size (Methods)

⁴ K = observed MSE/expected MSE and describes the amount of phylogenetic signal (larger indicates less variation explained by phylogeny; 1.00 is expected under Brownian motion character evolution)

⁵ p is probability that the sample conforms to Brownian evolution with p less than 0.05 indicating a significant phylogenetic signal

for female body mass), population density was negatively related to female home range size ($F_{2,19} = 10.22$, $p = 0.0025$). Results failed to find a significant relationship between female body mass among species with or without delayed implantation using analysis of covariance ($F_{2,33} = 1.19$, $p = 0.42$).

Next, we tested for the directional cause and effect of environment, population density, home range size, and delayed implantation (Table 2). The best model of 24 tested supported that species living in highly seasonal environments exist at relatively low densities and use relatively larger areas (home range size), which in turn related to presence of delayed implantation (Fig. 2). Conversely, species living at lower latitudes with low seasonality were associated with greater densities, smaller home range size, and the loss of delayed implantation as a reproductive mechanism. Other supported models indicated similar relationships for primary productivity, latitude, and snow, but with somewhat less statistical support (Table 2). Here, lower primary productivity, higher latitudes, and greater snowfall were related to lower population density, greater home range size, and the evolution of delayed implantation.

Discussion

Adaptations by mustelids to seasonality include larger annual ranges, lower population density, and the evolution of delayed implantation. Mammals give birth and raise young when conditions are favourable; however for high latitudes the favourable season often is brief and parturition early in the growing season results in a winter mating season. For species living at higher latitudes and with a gestation length that results in mating occurring during winter, opportunities for meeting members of the opposite sex are reduced due to extensive home ranges

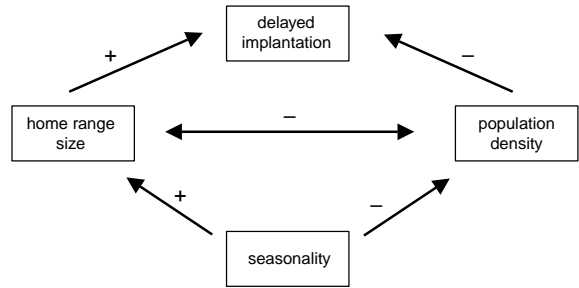


Fig. 2. Structural equation models representing the relationships among explanatory variables influencing delayed implantation for 34 species of the mammalian family Mustelidae. The model variables were developed using the covariance matrix and arrows depict the proposed links between variables (Table 2). Positive (+) and negative (-) parameterized regression coefficients are associated with each link. Error terms are not included in the structural equation diagrams. The coefficients were parameterized using iterative normal-theory maximum likelihood (SAS, 1999).

and low population density. Thus, high latitude environments decrease the opportunity for male and female interactions during the mating season. However, the evolution of delayed implantation decouples the timing of parturition and mating allowing both to occur during the same optimal summer season (Sandell 1990, Ferguson et al. 1996).

The evolution of delayed implantation in mammals has received much recent attention in the literature (Ferguson et al. 1996, Baryshnikov et al. 2003, Lindfors et al. 2003, Thom et al. 2004), and its value for mammalian reproduction has received much emphasis, from physiological, anatomical, and evolutionary standpoints (Hamlett 1935, Mead 1989, Sandell 1990). The plethora of evolutionary hypotheses all centre on the central theme that delayed implantation enables the uncoupling of mating and parturition events, most likely so that both can occur at the optimal time under

Table 2. Comparison of structural equation models with $\Delta AIC_c < 2$ that predict environment (lat = latitude, seas = seasonality, pp = primary productivity, snow = snowfall, temp = temperature) either directly or indirectly (through population density and/or home range size) causes delayed implantation for 34 species of mustelids. For example, the best model (first on list) indicates that greater seasonality causes low population density which causes large individual home range size, which causes delayed implantation. Variables are standardized independent contrasts that control for phylogenetic effects and general linear models are forced through the origin (no intercepts).

Model rank (best to worst)	Chi-square ¹	P ²	AIC _c ³	Δ_i AIC _c ⁴	w _i ⁵
seas → den → hr → di	0.69	0.88	-3.93	0.00	0.136
pp → den → hr → di	0.90	0.83	-3.72	0.21	0.123
seas → hr → den → di	1.20	0.75	-3.42	0.51	0.106
lat → den → hr → di	1.27	0.74	-3.35	0.58	0.102
lat → hr → den → di	1.39	0.71	-3.23	0.70	0.096
pp → hr → den → di	1.44	0.70	-3.18	0.75	0.094
snow → hr → den → di	2.16	0.54	-2.47	1.46	0.066

¹Chi-square measure is the optimum function value F multiplied by (N-1)

²A higher p value indicates a more reliable model

³AIC_c = second order Akaike information criteria ($AIC = n \log(\sigma^2) + 2K$) bias adjusted AIC for small sample size = $AIC + (2K(K+1))/(n-K-1)$ where K is the total number of estimated regression parameters including σ^2 (no intercept) and n is sample size

⁴ Δ_i = AIC differences computed as $AIC_i - AIC_{\min}$

⁵w_i = $\exp(-1/2\Delta_i) / \sum \exp(-1/2\Delta_i)$

environmental constraints associated with environments that vary in space and time (Sandell 1990, Ferguson et al. 1996).

The role of environmental constraints on life history evolution is well understood (Stearns 1992), and its effects on animal reproduction increasingly documented (Berven and Gill 1983, Reznick 1985, Larivière and Ferguson 2002, 2003, Ferguson and Larivière 2004a). However, there is a lack of consensus about the linkage between environmental seasonality and delayed implantation (Lindenfors et al. 2003, this study). The main suggestion of Lindenfors et al. (2003) is that analyses among carnivores should be restricted to the Mustelidae, since gains or losses of delayed implantation occurred mostly within this family.

Previously, Ferguson and Larivière (2004b) found that mustelids differed from other carnivores in a number of ways: male home range size was larger, population density lower, seasonality greater, duration of oestrus longer, and sexual size dimorphism greater. Our structural equation analyses with data from the world's mustelid species reveal links between environmental seasonality and the evolution or retention of delayed implantation in the Mustelidae. Also, the environmental parameters latitude, primary productivity, and snowfall related to whether mustelids evolved or lost delayed implantation. This suggests that although seasonality, as defined here, may not be the main force behind retention or evolution of delayed implantation, it is likely that environmental conditions (Ferguson et al. 1996, Thom et al. 2004) led to the evolution of delayed implantation in mustelids (and conversely adaptation to more southern latitude environments may have led to the loss of delayed implantation). Seasonality was correlated with latitude, primary productivity, and snowfall, so it is not surprising that model support was similar for the four variables. Nonetheless the best model incorporated seasonality.

One possible reason for the divergence of opinions regarding seasonality is how seasonality is defined and calculated. Seasonality is defined as the fluctuation of environmental conditions that directly affect primary productivity on the earth's surface (Boyce 1979, Lindstedt and Boyce, 1985). Variability in primary productivity is thus the crucial measure of seasonality, and the measure that should be used in evolutionary investigations. Lindenfors et al. (2003) used "birth season" as their seasonality variable, and concluded "...seasonality cannot explain the absence/presence of delayed implantation in carnivores" (Lindenfors et al. 2003: 1955). However, birth season is influenced not only by true environmental seasonality, but also by other environmental gradients such as latitude and precipitation. Thom et al. (2004) used latitude as a surrogate for seasonality and concluded that their "...analyses supported the hypothesis that delayed implantation is more

prevalent in seasonal climates" (Thom et al. 2004: 175). Seasonality, defined as the variation in environmental conditions within a year's time, is a variable independent of biological events. For example, if animals with delayed implantation have a more variable birth season (Lindenfors et al. 2003), then is it their parturition date that is more variable (biological variable), or is it the seasonality of the environment that the animals occupy (environmental variable).

Mate choice is a fundamental component of mammalian mating and is typically exercised by the sex with the greater reproductive investment. In most mammals, females produce a large zygote and placental young. Thus, females have more to lose in choosing to mate with a low quality male and mate choice is typically stronger in females than males. However, for solitary species that are wide ranging, the ability of females to compare males is limited, as encounters with members of the other sex are restricted by density and range size. One option for females may be to mate during a season with greater opportunities of meeting mates (i.e. evolution of delayed implantation) and then mate with multiple partners and allow for internal sperm competition (Clutton-Brock and Parker 1995, Larivière and Ferguson 2003).

The evolution of delayed implantation is possibly related to a reduction in the number of litters per year or small body size (Lindenfors et al. 2003). In the Mustelidae, only the least weasel (*Mustela nivalis*) can produce multiple litters within a year and for other species with delayed implantation, loss of the first litter may lead to subsequent pregnancy (Erlinge 1979). Even Mustelid species in tropical environments typically produce only one litter annually. The evolution of delayed implantation may relate to the benefits gained by extending pregnancy, considering that pregnancy is both energetically demanding and that it may negatively affect an individual's survival. Additionally, Lindenfors et al. (2003) used small body size as a surrogate for the presence of life history traits such as short life spans, unpredictable adult mortality and multiples litters, traits also associated with species that are "reproducers" (Ferguson and Larivière 2002), and also for species that occur at more southern latitudes (Ferguson and Larivière 2004a).

Understanding the ecological factors that determine the prevalent reproductive system of a species, such as seasonality favoring the evolution of delayed implantation, is central to evolutionary biology. This is because the environment influences mating systems, which ultimately determine patterns of gene transmission across generations and thus genetic diversity, speciation, and extinction (Schwartz et al. 2002). The evolutionary consequences of sexual selection in seasonal environments likely select for greater genetic variation and faster evolution (Møller 1998, Wright et al. 2003, Pawar 2005). Under the circumstances of large range size and small

population density, the effective population size of northern carnivores is small, thereby increasing the risks associated with anthropogenic changes that include fragmentation and global warming. A conservation outcome of the evolution of particular reproductive strategies adapted to seasonal environments is the need to preserve space for gene flow among disparate populations to retain genetic diversity and prevent local population extinctions within a metapopulation context. Thus, understanding the environment–life history connection has management and conservation implications of crucial importance for the maintenance of biodiversity.

Lindenfors et al. (2003) clearly highlight the need for better data on the presence or absence of delayed implantation in poorly-known species and make a good argument that mustelids without delayed implantation may have lost delayed implantation over evolutionary time. Additionally, we provide structural equation model evidence supporting the role of environmental variables in the evolution or maintenance of delayed implantation for species living with greater seasonality, or its loss in species occupying less seasonal environments. Life history traits of Mustelidae suggest that, once we control for phylogenetic effects, the environmental pressures associated with life in northern environments, be they seasonality, primary productivity, snowfall or latitudes (Thom et al. 2004), emerge as the unifying theme in environmental traits characterizing mustelids with delayed implantation.

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