

# Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores<sup>1</sup>

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**Abstract:** Researchers have put forth many explanations for the evolution of delayed implantation (DI) in mammals. Our results support the seasonality hypothesis which predicts that mammalian carnivores living in highly seasonal environments are more likely to have evolved DI. By uncoupling the time constraint between conception and parturition, DI allows females to track environmental conditions more closely. The selective advantage of DI in seasonal environments is for an earlier date of parturition (1.5 months) and a possible link between body condition and timing of birth. We used a phylogenetic correction method in conjunction with analysis of covariance to describe allometric grade shifts in life history traits associated with the presence/absence of DI in 52 species of North American carnivores. The grade shift approach partitions the phylogenetic (slope) and ecological (elevation) factors driving variation in life history traits. Correcting for phylogeny and body mass, we demonstrated a grade shift in gestation length and neonate mass. Terrestrial species with DI have a relatively shorter gestation length and smaller neonates than terrestrial species without DI, while marine species with DI have relatively longer gestation and larger neonates than the former two groups. The results also suggest that terrestrial carnivores with DI, living in seasonal environments, have evolved reduced maternal energy expenditure (shorter gestation, smaller neonates and smaller litter size) as a trade-off to spread out the risk of reproductive failure (later maturation, longer birth interval and possibly longer life). We hypothesize that (1) grade shift differences in life history traits initially evolved in highly seasonal environments; (2) the evolution of DI secondarily promoted a disassociation of the various parts in the life history module dealing with the timing of life history events; and (3) differing trophic dynamics associated with marine and terrestrial environments favoured selection for the direction of life history grade shift changes.

**Keywords:** carnivores, comparative method, delayed implantation, grade shifts, seasonality, life history.

**Résumé:** De nombreuses explications ont été proposées pour rendre compte de l'évolution de l'implantation différée (ID) chez les mammifères. Nos résultats viennent appuyer l'hypothèse dite de la saisonnalité, selon laquelle les carnivores mammaliens, vivant dans des environnements où la saisonnalité est marquée, auraient connu une évolution favorisant l'apparition de l'ID. En dissociant dans le temps le moment de la conception et celui de la mise-bas, l'ID permet aux femelles de s'ajuster plus finement aux conditions de l'environnement. L'avantage que procure l'ID au plan de la sélection, dans des environnements à fort contraste saisonnier, concerne la mise-bas hâtive (1,5 mois) et la relation unissant probablement la condition physique et le moment de la naissance. Nous avons utilisé une méthode de correction phylogénétique ainsi qu'une analyse de covariance pour décrire les changements de niveau dans les caractères de développement associés à la présence/absence de l'ID, chez 52 espèces de carnivores en Amérique du Nord. Cette démarche selon les niveaux de changement permet de distinguer les facteurs phylogénétiques (pente) et écologiques (altitude) entraînant des variations dans les caractères de développement. En apportant une correction pour la phylogénie et la masse corporelle, nous avons pu montrer un niveau de changement dans la durée de la gestation et la masse des nouveaux-nés. Les espèces terrestres connaissant une ID ont une période de gestation relativement courte par comparaison aux espèces terrestres sans ID et leurs nouveaux-nés sont de plus petite taille. Les espèces marines avec ID ont une période de gestation relativement longue par rapport aux deux groupes précédents et leurs nouveaux-nés sont de plus grande taille. Nos résultats indiquent aussi que les carnivores terrestres avec ID, vivant dans des environnements à contraste saisonnier, ont évolué vers une réduction de la dépense en énergie par la mère (gestation plus courte, nouveaux-nés de plus petite taille et portée plus petite), de façon à mieux répartir les risques d'un échec au plan de la reproduction (maturation plus longue, intervalle plus long entre les naissances et peut-être durée de vie accrue). Nous formulons l'hypothèse selon laquelle (1) les différences dans le niveau de changement des caractères de développement sont apparues dans des environnements à contraste saisonnier marqué; (2) l'évolution vers l'ID a favorisé en second lieu une dissociation des diverses étapes du développement, par un meilleur arrimage des événements marquant ce développement; et (3) la différenciation d'une dynamique trophique propre aux milieux marin et terrestre a favorisé un type de sélection qui a orienté le niveau de changement dans le développement.

**Mots-clés:** carnivores, méthode d'analyse comparée, implantation différée, niveau de changement, saisonnalité, développement.

## Introduction

Differentiating between phylogenetic and ecological forces involved in the evolution of life histories has provided the impetus for numerous theoretical and empirical studies (Boyce, 1988; Stearns, 1992; Roff, 1992) as well as controversy (Westoby, Leishman & Lord, 1995a; Harvey, Read &

Nee, 1995a). The use of allometry to describe the variation associated with life history characteristics is common in investigations of evolutionary ecology at the species level (Harvey, 1982; Peters, 1983; Calder, 1984). Interspecific comparisons, however, may generate questionable results due to their combining of environmental and phylogenetic effects (Harvey & Mace, 1982). Numerous methods have

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been designed to disentangle a species' history from adaptation to local environments (Felsenstein, 1985; Harvey & Pagel, 1991; Gittleman & Luh, 1992; Garland & Adolph, 1994).

The grade shift approach distinguishes between physical conditions (allometric slope) representing phylogenetic history, and ecological conditions (allometric elevation) representing evolutionary adaptation to current environments. Allometric grade shifts can be defined as log-linear relationships of body mass whereby the allometric coefficients differ among groups while the exponents remain approximately equal (Martin, 1984). For example, Martin & MacLarnon (1985) examined the relationship between gestation period and maternal body mass and described a sharp separation or grade shift between altricial and precocial mammals (but see Zeveloff & Boyce, 1986). The grade shift approach helps to separate the phylogenetic and ecological aspects of processes. The physical determines the slope of the regression between life history traits and standard measures (*i.e.* phylogenetic history), while the biological and ecological properties determine the elevation ( $y$ -intercept value; see Gautestad & Mysterud, 1993). Therefore, small to large animals show the same log-linear expansion (allometric slope), but may evolve quite different life history patterns represented by shifts in elevation.

We have used the grade shift approach to describe life history shifts associated with the adoption of delayed implantation (DI) in North American carnivores. DI is a reproductive mechanism found in numerous mammalian taxa including Edentata, Marsupialia, Rodentia, Chiroptera, Carnivora (includes Pinnipedia; Flynn, 1988), Insectivora, and at least one species (roe deer, *Capreolus capreolus*) of Artiodactyla (see reviews by Wimsatt, 1975; Renfree & Calaby, 1981; Sandell, 1990; Mead, 1993). Previous studies have primarily focused on the physiology and hormonal control of DI (Mead, 1981; 1993). Other researchers have investigated factors influencing implantation date such as food intake (Shapira *et al.*, 1974), photoperiod (Pearson & Enders, 1944; Mead, 1971), and temperature (Canivenc & Bonnin, 1981). However, the adaptive significance of DI remains controversial. It has been suggested that DI confers an advantage upon species living in extreme climatic conditions (Vogel, 1981). More specific explanations for the evolution of DI are that it provides species with a mechanism to give birth when conditions are energetically optimal (Ealey, 1963; Canivenc & Bonnin, 1981; Sandell, 1984), or allows greater flexibility between timing of mating and parturition (Conaway, 1971; Sandell, 1990). Finally, DI has been suggested as a vestigial characteristic for some species with no contemporary adaptive value (see Hamlett, 1935; Enders, 1981; King, 1984; Sandell, 1990).

The ecological determinant for the evolution of DI may be correlated, at least indirectly, with the degree of seasonal variation in environmental conditions experienced by species (seasonality hypothesis). We examined this hypothesis using North American carnivores. Of the two forms of DI discussed by Sandell (1990), we consider only the seasonal or obligate DI found in all pinnipeds and some terrestrial carnivores where gestation spans most of the year, and the delay is usually long. We define gestation

length as the period of time between implantation of the blastocyst and parturition. We have chosen North American carnivores for a comparative study because almost half of the species exhibit obligate DI (25 of 52), and because the geographic distribution of these species encompasses a wide range of seasonal environments.

We hypothesize that carnivore species evolved DI in seasonal environments in response to the advantages afforded by a shift in the timing of certain life history traits, notably gestation length. DI likely relaxes the time constraints associated with the timing of breeding, gestation, and parturition. The proximate explanation linking DI and the life history traits of birth events (gestation length, neonatal mass, and litter size) is likely embryological (Mead, 1989). Here we test the seasonality hypothesis and discuss ultimate explanations for the evolution of DI and the grade shift in life history traits for North American carnivores.

## Materials and methods

### DATA SOURCES

Reproductive and life history data for each species were collected primarily from Gittleman (1986), Nowak (1991), and articles from "Mammalian Species". Other sources included Novak *et al.* (1987), Mead (1989), Reidman (1990) and Bonner (1990). A complete list of references and scientific names is presented in Appendix I.

### TAXONOMY AND PHYLOGENY

The following is a description of the sources used to construct the "best current compromise" phylogeny (Figure 1). Specific taxonomy of North American carnivores followed Wilson & Reeder (1993). Phylogeny of the Carnivora was reconstituted from divergence times available for each family (Garland *et al.*, 1993), and modified using data from the fossil record (Savage & Russell, 1983). Phylogenies for the felids (Collier & O'Brien, 1985), mustelids (Bryant, Russel & Fitch, 1993), canids (Wayne & O'Brien, 1987; Wayne, 1993), ursids (Goldman, Giri & O'Brien, 1989), phocids (Sarich, 1969; Perry *et al.*, 1995), and procyonids (Decker & Wozencraft, 1991) were based on recent phylogenetic analyses for each family, and again complemented using occurrence in the fossil record (Savage & Russell, 1983). Pinnipeds were considered monophyletic (Flynn, 1988; Flynn, Neff & Tedford, 1988; Wyss, 1988). Eastern and western populations of the spotted skunk (*Spilogale putorius*) were treated separately because of their differences in distribution and presence/absence of DI (Appendix I). The data set consisted of 5 families, 22 genera, and 39 species of terrestrial carnivores (including the sea otter), and 3 families, 9 genera, and 13 species of marine carnivores (Pinnipeds).

### SEASONALITY INDEX

The degree of seasonality may be defined by the relative deviation from mean annual climatic conditions (Boyce, 1978). As a measure of seasonality, Zeveloff (1982) computed the coefficient of variation (CV) among monthly actual evapotranspiration (AET) values of an average mean of long-term (approximately 30 years) temperature and precipitation records. Zeveloff (1982, see also Zeveloff &

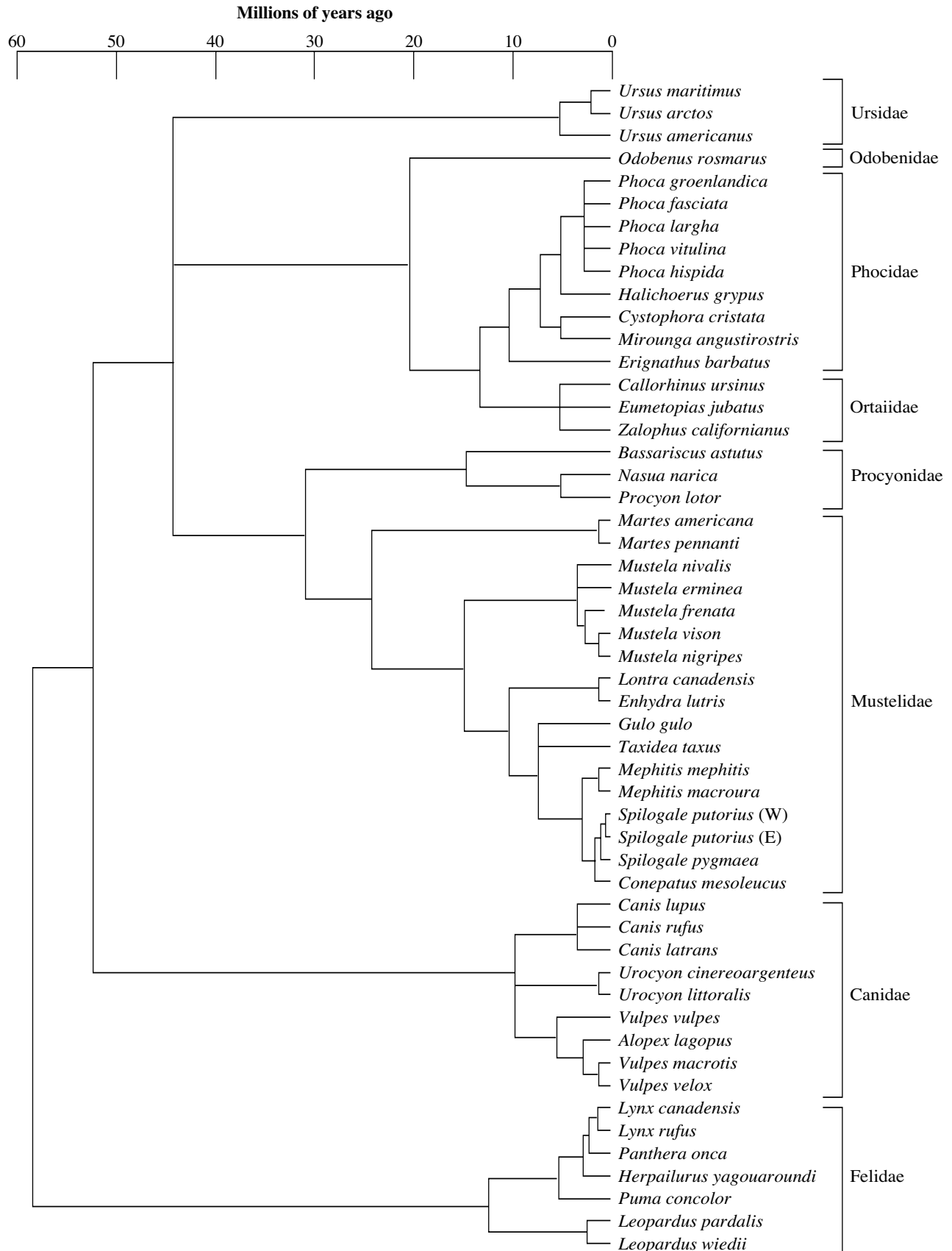


FIGURE 1. Phylogenetic relationship for 52 species of North American carnivora.

Boyce, 1988) randomly selected 102 sample points from a map of North America including Mexico. The water balance method allows estimation of actual evapotranspiration (AET) from meteorological records and a few observations on the soil and vegetation (Dunne & Leopold, 1978). AET values calculated from the water balance method using the Thornthwaite approach (Thornthwaite & Mather, 1957) are correlated with primary productivity of vegetation (Rosenzweig, 1968a). Therefore, our seasonality variable measures the relative variation in primary productivity among months of an average year.

We determined the mean measure of seasonality by overlaying historical distribution maps of North American carnivore species (Novak *et al.*, 1987) and 102 weather station sampling locations (Zaveloff, 1982) using IDRISI Geographic Information System (Eastman, 1990). For marine carnivores we used the seasonality values for the closest coastal weather stations since estimation of AET is a land-based method. We then calculated the mean of the overlaid individual values of seasonality (CV of AET) within a species' geographic distribution. Seasonality values greater than 1 indicate greater than average seasonal variation and values less than 1 indicate relatively small monthly differences. This relationship generally followed a latitudinal pattern of greater seasonality for species living farther north.

#### STATISTICAL ANALYSES

We used empirically scaled, computer-simulated data to obtain "phylogenetically correct" distributions of  $F$  statistics for testing hypotheses of differences between groups (*e.g.* with and without DI). Phylogenetic analysis was performed using PDTREE, PDSIMUL and PDANOVA (Garland *et al.*, 1993) and was applied to the proposed phylogenetic topology and branch lengths for the carnivore species under study (Figure 1). This comparative method views two continuous traits as evolving along a phylogeny and simulates changes to the traits as two random variables drawn from a bivariate normal distribution (Martins & Garland, 1991). Specifying a phylogenetic topology is required for phylogenetic based methods that test evolutionary correlations (Felsenstein, 1985).

We used the simplest null model for the evolution of continuous traits; gradual Brownian motion. This model simulates random genetic drift with no selection and postulates that successive changes of a character are independent of each other and of the character's starting value. Other models of evolution were tested (specification Brownian motion and Ornstein-Uhlenbeck process) as a type of sensitivity analysis but results did not change significantly. No explicit limits on how large or small a character can evolve (*e.g.* minimum and maximum female body mass) were incorporated in our analysis, which makes our tests more conservative. Checks of branch lengths as described in Garland, Harvey & Ives (1992) were used and results indicated no significant relationships for all ten traits, including body mass, between the absolute values of standardized contrasts with their standard deviations ( $r < 0.1$ ).

Using the specified phylogenetic topology, branch lengths, and model of evolutionary change, PDSIMUL ran

1 000 computer simulations. For each set of simulated tip data (body mass and nine life history traits) various statistics were computed and empirically scaled null distributions formed the basis for hypothesis testing. The SAS statistical package was used to read in the ASCII file of  $F$ -ratios and compute the 95th percentile of this distribution. If the ratio for the real data set exceeded the critical level of the empirical null distribution ( $P$ -value  $< 0.05$ ), we concluded that the three groups (terrestrial carnivores without DI, terrestrial with DI, and marine with DI) differed significantly in the life history trait with body mass as the covariate.

We used simple descriptive statistics from nested ANOVAs to inform whether phylogenetic correlation occurred within a given trait. Nested ANOVA analyses are not useful for inferring causation or process (Harvey & Pagel, 1991). But, if comparative data are statistically independent and no phylogenetic correlation was evident from a nested ANOVA procedure, then a conventional comparative analysis can be performed without more sophisticated comparative methods (Gittleman & Luh, 1992).

All life history data were logarithmically transformed prior to analysis (see Harvey, 1982) except seasonality, parturition date, and litter size. All statistical analyses were performed using the SAS statistical package for microcomputers.

## Results

#### SEASONALITY AND DELAYED IMPLANTATION

The seasonality index for terrestrial species with DI ranged from 0.88 to 1.51 with a mean ( $\pm 1$  SD) of  $1.10 \pm 0.19$  ( $n = 11$ ) and marine species with DI ranged from 0.74 to 1.64 with a mean of  $1.21 \pm 0.27$  ( $n = 14$ ). In contrast, species without DI experienced a mean seasonality index of  $0.87 \pm 0.25$  with a range of 0.38 - 1.51 ( $n = 27$ ). The mean seasonality indexes of the three groups were statistically different ( $F_{2,51} = 9.10$ ,  $P < 0.01$ ). Lower than average seasonality values for species with DI were recorded for one species from Ursidae (black bear), and three species from Mustelidae (badger, long-tailed weasel, western spotted skunk). Greater than average seasonality values for species without DI were recorded for four species from Canidae (arctic fox, red fox, swift fox, wolf), one species from Procyonidae (raccoon), four species from Mustelidae (black-footed ferret, least weasel, mink, striped skunk), and one species from Felidae (lynx).

We found significant differences in parturition dates for the three groups after statistically controlling for the effect of seasonality ( $F_{2,45} = 3.37$ ,  $P = 0.01$ ). Terrestrial species with DI (15 March) gave birth approximately 45 days earlier than species without DI (1 May) and 30 days earlier than marine carnivores with DI (15 April).

#### GESTATION LENGTH AND DELAYED IMPLANTATION

Regression of gestation length on female mass generated significant relationships for terrestrial species without DI ( $F_{1,26} = 39.8$ ,  $P < 0.01$ ,  $r^2 = 0.61$ ), terrestrial species with DI ( $F_{1,10} = 28.3$ ,  $P < 0.01$ ,  $r^2 = 0.76$ ), and marine species with DI ( $F_{1,13} = 4.6$ ,  $P = 0.05$ ,  $r^2 = 0.28$ ). The lower  $r^2$ -value for species without DI is due partially to the position

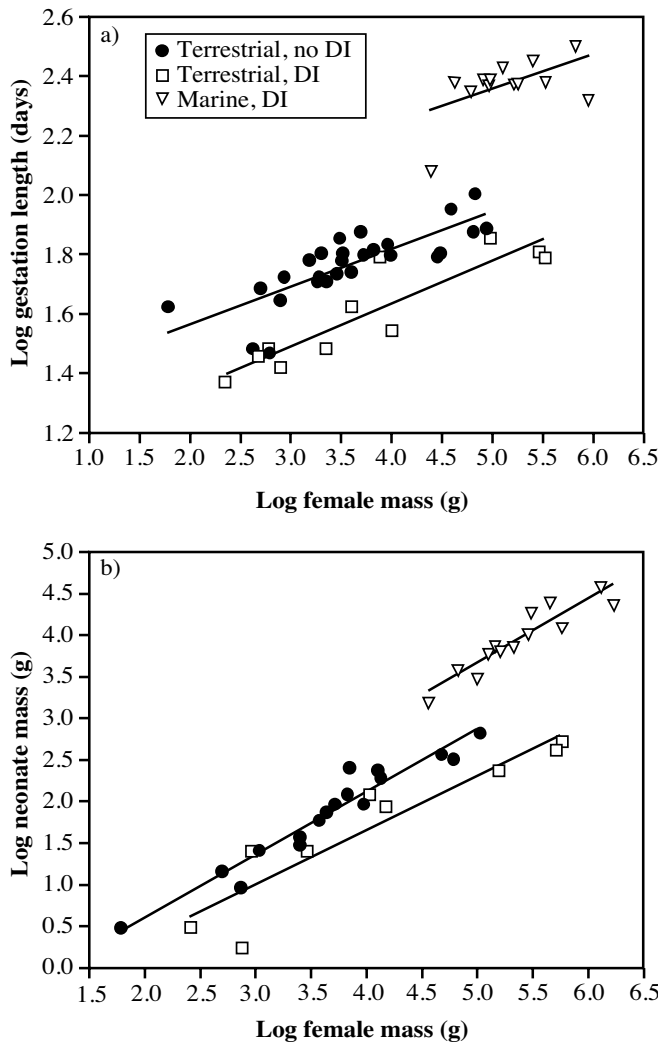


FIGURE 2. Regression of gestation length (a) and neonate mass (b) on female body mass after log transformation for 27 terrestrial carnivores without delayed implantation (DI), terrestrial carnivores with DI ( $n = 11$ ) and marine carnivores with DI ( $n = 14$ ) from North America.

of eastern spotted skunk and mink (Figure 2a). These two species would likely fit better on the regression for species with DI. But since both species have a relatively short and highly variable period of DI we decided *a priori* to classify them with species lacking DI (see Appendix I). Sea otters exhibit DI but they do not fit on the 'terrestrial with DI' regression line (Figure 2a). This outcome may be related to the marine environment that this species occupies and therefore we grouped the 12 North American species of Pinnipeds (marine carnivores with DI) along with the sea otter. Results from ANCOVA indicated that the slopes for the three regressions were not significantly different ( $F_{2,51} = 0.24, P > 0.50$ ). However, elevation estimates ( $\pm 1$  SE) for terrestrial species without DI ( $1.27 \pm 0.08, n = 27$ ), terrestrial species with DI ( $1.16 \pm 0.07, n = 11$ ), and marine species with DI ( $1.79 \pm 0.23, n = 14$ ) were statistically different ( $F_{2,51} = 115.0, P < 0.01$ ). Thus, there exists grade shifts (similar allometric slope, different elevation) in gestation length between terrestrial species with and without DI and marine species with DI (Figure 2a).

NEONATE MASS AND DELAYED IMPLANTATION

Regression of neonatal mass on female mass generated significant relationships for terrestrial species without DI ( $F_{1,16} = 207.9, P < 0.01, r^2 = 0.93$ ), terrestrial species with DI ( $F_{1,8} = 143.5, P < 0.01, r^2 = 0.95$ ), and marine species with DI ( $F_{1,13} = 73.7, P < 0.01, r^2 = 0.86$ ; Figure 2b). Results from ANCOVA indicated that the slopes for the three regressions were not significantly different ( $F_{2,37} = 3.22, P = 0.06$ ). Again, elevation estimates ( $\pm 1$  SE) for terrestrial species without DI ( $2.36 \pm 0.05, n = 17$ ), terrestrial species with DI ( $2.02 \pm 0.06, n = 9$ ), and marine species with DI ( $3.37 \pm 0.06, n = 14$ ) were statistically different ( $F_{2,37} = 108.6, P < 0.01$ ). Therefore, a grade shift also occurs in neonatal mass among the three groups, but the marginal significance in testing for differences in slopes does not rule out other possible explanations.

PHYLOGENETIC CORRECTION AND GRADE SHIFTS

Comparing relative variance components from nested ANOVAs suggested that most of the variance for each of the nine life history traits occurred among genera within family (Table I). The notable exception was seasonality index which equally split the variance between species within genera and genera within family. Therefore, for seasonality the use of a phylogenetic correction method is likely not justified. Gestation length, neonatal mass and longevity each had greater than 80 percent of the total variance explained at the higher taxonomic level indicating a large phylogenetic component. The other five life history traits showed variance partitioning between these two extremes.

TABLE I. Comparison of relative variance (nested ANOVA) calculated for 3 taxonomic levels (52 species; 23 genera; 8 families) and nine life history traits recorded for species of North American Carnivora

Life history trait	Nested ANOVA % of total variance component	
	Among species within genera	Among genera within family
Gestation length	12.4	87.6
Seasonality	49.3	50.7
Parturition date	27.5	72.5
Litter size	28.1	71.9
Neonate mass	9.3	90.7
Age of weaning	22.3	77.7
Age of maturation	33.5	66.5
Birth interval	34.5	65.5
Longevity	18.0	82.0

Using simulated data to obtain phylogenetic correct distributions, we found that only gestation length and neonate mass differed significantly among groups (terrestrial carnivores without DI, terrestrial carnivores with DI, and marine carnivores with DI; Table II). Nested ANOVA results indicate that for seasonality, conventional ANCOVAs are sufficient for comparative analyses. For the other six life history traits, our conclusions about a possible group difference was not significant when phylogenetic nonindependence was incorporated through computer simulation techniques. Since these life history traits fall somewhere between the two extremes, we view the

TABLE II. Analysis of covariance comparing nine life history traits of members of North American Carnivora with  $\log_{10}$  body mass as the covariate. Differences ( $\alpha = 0.05$ ) are analyzed as least squares means  $\pm 1$  SE ( $n =$  number of species) for terrestrial species without delayed implantation (DI), terrestrial species with DI, and marine species with DI. All variables, except seasonality, parturition date and litter size, were  $\log_{10}$  transformed. Critical values for  $F$  statistics and associated significance levels are presented for conventional values (assuming species represent independent data) and based on analysis of data simulated along the phylogeny shown in Figure 1 under the Brownian motion model of character change (Garland *et al.*, 1993)

Variable	No DI	DI terrestrial	DI marine	Conventional ANCOVA		Brownian model	
				$F$	$p$	Critical value	$p$
Gestation length	1.82 $\pm$ 0.02 (27)	1.64 $\pm$ 0.02 (11)	2.22 $\pm$ 0.03 (14)	115.0	< 0.01	33.9	< 0.01
Seasonality	0.88 $\pm$ 0.05 (27)	1.11 $\pm$ 0.08 (11)	1.19 $\pm$ 0.09 (14)	5.22	< 0.01	27.1	> 0.20
Parturition date	8.65 $\pm$ 0.54 (25)	5.71 $\pm$ 0.76 (11)	9.91 $\pm$ 0.87 (13)	7.73	< 0.01	31.2	> 0.20
Litter size	3.81 $\pm$ 0.25 (26)	3.04 $\pm$ 0.37 (11)	1.62 $\pm$ 0.40 (14)	8.83	< 0.01	26.5	> 0.20
Neonate mass	2.36 $\pm$ 0.05 (17)	1.98 $\pm$ 0.06 (8)	3.40 $\pm$ 0.06 (15)	116.9	< 0.01	25.8	0.01
Age of weaning	1.95 $\pm$ 0.11 (19)	2.11 $\pm$ 0.14 (9)	1.46 $\pm$ 0.14 (14)	4.85	0.01	25.4	> 0.20
Age of maturation	2.69 $\pm$ 0.06 (22)	2.90 $\pm$ 0.09 (9)	2.92 $\pm$ 0.08 (15)	3.00	0.06	25.7	> 0.20
Birth interval	2.61 $\pm$ 0.03 (21)	2.74 $\pm$ 0.03 (10)	2.52 $\pm$ 0.04 (14)	9.2	< 0.01	23.5	> 0.10
Longevity	3.72 $\pm$ 0.02 (23)	3.77 $\pm$ 0.04 (9)	3.84 $\pm$ 0.04 (12)	2.92	0.06	30.3	> 0.20

observed grade shifts with caution. For terrestrial species with DI, litter size was smaller than in terrestrial species without DI while age at maturity, interbirth interval, and longevity were longer (Table II). For marine species with DI, age of weaning and birth interval were lower than for terrestrial species while neonate mass, age of maturation and longevity were higher.

## Discussion

Answering why DI evolved in carnivores involves both seasonality and life history explanations. The first part of the DI explanation concerns the evolution of DI in highly seasonal environments where the female gains the advantage of flexibility in timing of conception and parturition. Since time of breeding and birth are likely a function of body condition and environmental conditions, uncoupling conception and parturition period would allow greater flexibility in the timing of reproductive events (Sandell, 1990). While photoperiod changes can indicate when the spring availability of food is most likely to occur each year (I'Anson *et al.*, 1991), body condition may give an index of current food availability, and allow females to calibrate the time of parturition according to environmental cues. Woodroffe (1995) showed that nutritional state of female European badgers prior to implantation influenced implantation date by up to 37 days, with females in good condition implanting relatively early. Such flexibility would enable females to better track environmental fluctuations and make adjustments regarding the timing of reproductive events. Controlling for seasonality, terrestrial carnivores with DI have earlier parturition dates relative to terrestrial species without DI. For carnivores with DI, giving birth early in the year likely provides a selective advantage over species without DI since these young will have a longer period of growth.

The second part of the DI explanation requires a description of the link between the presence/absence of DI in North American carnivores and a grade shift in several life history traits. Currently there is a debate over the applicability of phylogenetic correction methods (Westoby, Leishman & Lord, 1995a, b; Ackerly & Donoghue, 1995; Harvey, Read & Nee, 1995a, b). This controversy is important to the interpretation of our results since phyloge-

netic considerations indicate that only two of our nine comparisons are significant. Mousseau & Roff (1987) found that the heritability estimated for a life history trait depended on the population of origin and environmental conditions. Heritabilities varied from 0 to 1.0, with values over 30 percent frequently coming from natural populations. The conclusion is that there was plenty of genetic variation present for life history traits to evolve in natural populations.

Comparative phylogenetic methods may overrepresent historical constraint when statistically controlling for the lack of independence among individual species values (Westoby, Leishman & Lord, 1995a; Ackerly & Donoghue, 1995). We expect life history traits to comprise a continuum as to the relative involvement of ecological (short temporal evolution) and phylogenetic (long temporal evolution) selection. For example, gestation length and neonatal mass are likely maintained by strong selection resulting in high heritability and these traits would therefore have a larger phylogenetic component. This expectation was supported by nested ANOVA results that show gestation length and neonate mass to have the strongest phylogenetic component represented by a greater variance component within family (Table I). Variation in gestation length due to environmental factors is both rare and limited in mammals (Racey, 1981). In contrast, life history traits such as parturition date and age of maturation and behavioural traits such as habitat selection (*e.g.* seasonality index) would have a flat fitness profile (*sensu* Stearns & Crandall, 1981) and phenotypic variation around the optimum would be large (Bateson, 1988). This expectation was also supported by nested ANOVA results that imply species values for the seasonality index are independent. We would expect these latter life history traits to have larger ecological components and phylogenetic correction may not be an appropriate procedure (Westoby, Leishman & Lord, 1995b).

Many behavioural and ecological traits show considerable plasticity and minimal phylogenetic correlation (*e.g.* home range size: Gittleman & Harvey, 1982; and population density: Damuth, 1981). Therefore, for these variables we consider the relative significance of comparisons should lie somewhere between the simulated  $F$ -values based on phylogeny and the least squares results based on the assumption of independence of data values. Unfortunately, without information on the fitness profiles of these traits for

natural populations, we do not know how well this explanation accounts for the phenotypic variations observed (Gittleman & Luh, 1992). Our conclusions regarding grade shifts in life history traits relative to the presence of DI must remain necessarily tentative.

Marine carnivores (sea otter and Pinnipedia) with DI display a strikingly different shift in gestation length and neonatal mass compared to terrestrial carnivores with DI. Marine carnivores have a relatively longer gestation length (allometric coefficient,  $a = 1.8$  versus those terrestrial species without DI,  $a = 1.3$  and those with DI,  $a = 1.2$ ) and larger neonates (allometric coefficient,  $a = 3.4$  for marine carnivores versus terrestrial species without DI,  $a = 2.4$  and terrestrial species with DI,  $a = 2.0$ ). Pinnipeds likely evolved from a high latitude carnivore (Reidman, 1990) that had probably already evolved DI as an adaptation to seasonal environments. But seals may have maintained DI for other reasons. Sandell (1990) argues that DI allows mating to occur during the period of maximum food availability (mate choice hypothesis). An alternative hypothesis is that mating will occur during the period when neonates would be most susceptible to mortality. The assumption here is that mating at this time will reduce inter- and intraspecific predation of neonates due to the presence of courting males. Another hypothesis suggests that DI allows pinnipeds to give birth and breed at about the same time each year, which for some pinnipeds coincides with the period when they are on land.

Terrestrial and marine carnivores with DI display opposite grade shifts in gestation length and neonatal mass and researchers have proposed different hypotheses to explain the pattern of marine carnivores giving birth to relatively more precocial young (see Kovacs & Lavigne, 1988). One hypothesis suggests that marine carnivores give birth to relatively larger and more developmentally mature neonates because of the thermal advantage in cold environments (Laws, 1959). We propose that selection for relatively "altricial or precocial" life history traits in carnivores is correlated with the susceptibility of neonates to predation (extrinsic mortality; *sensu* Medawar, 1952). High latitude marine carnivores live in a 5-level trophic ecosystem (Welch *et al.*, 1992) in contrast to the 3-level terrestrial system (Hairston & Hairston, 1993). Shorter gestation length and smaller neonates accrue advantages for terrestrial carnivores living at, or near the top, of the food web. In contrast, longer gestation length and larger young are likely advantageous for marine carnivores, which are themselves prey for higher predators. Whatever the explanation, the adoption of a relatively "precocial or altricial" life history in marine or terrestrial carnivores, respectively, appears to be facilitated by the evolution of DI.

Seasonality may help answer why life history grade shifts evolved in carnivores. The amount of variation in demographic parameters, such as juvenile mortality, attributed to density-independent factors increases in highly seasonal and unpredictable environments (Rosenzweig, 1968b; Boyce, 1978; Boyce, 1979; Lindstedt & Boyce, 1985). Increases in mean and variance of juvenile mortality are associated with a longer reproductive lifespan (Murphy, 1968; Schaffer, 1974; Orzack & Tuljapurkar, 1989). Therefore, carnivore species inhabiting unpredictable

environments may maximize fitness by decreasing energetic costs during reproduction and increasing the number of reproductive events. Our results suggest that carnivores with DI and living in seasonal environments have evolved such a trade-off. Comparing the life histories of terrestrial carnivores with and without DI, while controlling for body mass, we found a decrease in maternal energy expenditure for those species with DI through shorter gestation length, smaller neonates, and smaller litters (Table II). A spreading out of reproductive risk is also suggested by delayed sexual maturation and longer interbirth interval. How animals decrease one set of life history traits (gestation length, neonate mass and litter size) while increasing others (age of maturation, interbirth interval, and longevity) can only be explained by a disassociation of the two components. The construction of separable modules, such as the timing of life history events, can arise in any complex system through natural selection (Gould, 1992; Fodor, 1983).

Our results support the seasonality hypothesis for the evolution of DI in carnivores inhabiting North America. Although differences in seasonality and parturition date are not significant while controlling for phylogeny, we expect these variables to be under strong environmental selection and to show evolutionary change on an ecological scale rather than a phylogenetic scale. Therefore, phylogenetic correction methods may not be necessary. The second finding suggests that the evolution of DI is associated with life history grade shifts in North American carnivores. Here only gestation length and neonate mass had a significant shift in allometric coefficients while controlling for phylogeny and body mass. Other life history traits may actually be unrelated to the presence/absence of DI in carnivores but we predict that a broader data base will indicate significant grade shifts in these life history traits as well. Statistical power can be increased by adding data from other clades of mammals and broadening the geographic base to include Eurasian carnivores, thus increasing the number of independent DI transitions available for testing.

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## APPENDIX I. Life history variables and seasonality index for North American carnivores

FAMILY Species	DI <sup>3</sup>	Female mass (g)	Seasonality index	Birth range	Gestation period (days)	Litter size	Neonate mass (g)	Weaning age (days)	Maturation age (days)	Interbirth interval (days)	Longevity (days)
<b>URSIDAE<sup>1</sup></b>											
<i>Ursus maritimus</i> <sup>a</sup>	Y	320 000	1.513	Dec. - Jan.	62	1.9	642	776	1 734	731	12 419
<i>U. arctos</i> <sup>b</sup>	Y	298 500	1.119	Jan. - Feb.	63	2	500	724	1 338	913	9 253
<i>U. americanus</i> <sup>c,d</sup>	Y	97 000	1.036	Jan. - Feb.	70	2.5	285	170	1 834	822	8 218
<b>ODOBENIDAE<sup>2</sup></b>											
<i>Odobenus rosmarus</i>	Y	690 000	1.641	April - June	315	1	58 000	676	2 008	1 278	12 784
<b>PHOCIDAE<sup>2</sup></b>											
<i>Phoca groenlandica</i>	Y	130 000	1.428	Feb. - March	267	1	10 000	12	1 825	365	12 784
<i>P. fasciata</i>	Y	95 000	1.480	April - May	234	1	9 400	32	1 278	365	10 958
<i>P. largha</i>	Y	80 000	1.519	Feb. - May	248	1	8 300	25	1 278	365	12 784
<i>P. vitulina</i>	Y	90 000	1.085	Feb. - Sep.	248	1	10 100	21	1 278	365	12 784
<i>P. hispida</i>	Y	62 500	1.595	March - April	225	1	4 100	50	1 825	365	15 706
<i>Halichoerus grypus</i>	Y	170 000	1.084	Dec. - Feb	236	1	14 900	21	1 460	365	16 802
<i>Cystophora cristata</i>	Y	180 000	1.130	Mar - Apr.	234	1	27 000	5	1 095	365	9 131
<i>Mirounga angustirostris</i>	Y	900 000	0.741	Dec. - March	210	1	33 600	28	1 460	365	7 305
<i>Erignathus barbatus</i>	Y	260 000	1.458	March - May	285	1	38 000	15	2 008	731	11 323
<b>OTARIIDAE<sup>2</sup></b>											
<i>Callorhinus ursinus</i>	Y	43 000	0.925	June - July	240	1	5 200	110	1 095	365	7 670
<i>Eumetopias jubatus</i>	Y	333 000	1.026	June - July	240	1	17 600	347	1 825	731	
<i>Zalophus californianus</i>	Y	82 000	0.888	May - June	240	1	8 300	269	1 643	365	7 305
<b>PROCYONIDAE<sup>1</sup></b>											
<i>Bassariscus astutus</i> <sup>c</sup>	N	870	0.791	May - June	52	3	28	71	300	365	2 922
<i>Nasua narica</i> <sup>l</sup>	N	5 000	0.663	June	74	4	140	89	1 020	365	6 209
<i>Procyon lotor</i> <sup>g</sup>	N	6 700	1.162	Feb. - June	65	3.8	106	120	540	365	3 653
<b>MUSTELIDAE<sup>1</sup></b>											
<i>Martes americana</i> <sup>h</sup>	Y	770	1.178	March - April	27	2.6	28	46	365	365	4 566
<i>M. pennanti</i> <sup>i</sup>	Y	2 250	1.117	March - April	30	2.7	28	63	730	365	3 653
<i>Mustela nivalis</i> <sup>j,k</sup>	N	53	1.204	March - Sep.	42	5.8	3	32	90	183	1 096
<i>M. erminea</i> <sup>k</sup>	Y	57	1.206	April - May	30	4.5	2	66	336	365	2 557
<i>M. frenata</i> <sup>k</sup>	Y	165	0.887	April - May	24	6	3	30	252	365	2 557
<i>M. vison</i> <sup>l</sup>	N <sup>4</sup>	610	1.097	April - May	29	5	9	28	420	365	2 922
<i>M. nigripes</i> <sup>k</sup>	N	800	0.969	May	44	3.5			315	365	4 018
<i>Lontra canadensis</i> <sup>m</sup>	Y	7 800	1.089	March - April	62	3	140	93	730	365	
<i>Enhydra lutris</i> <sup>n</sup>	Y	24 400	0.974	all year	120	1	2 100	363	1 095	365	
<i>Gulo gulo</i> <sup>o</sup>	Y	10 350	1.194	Jan. - April	35	2.8	99	71	630	822	5 661
<i>Taxidea taxus</i> <sup>p</sup>	Y	4 100	0.925	March - April	42	4		42	395	365	4 748
<i>Mephitis mephitis</i> <sup>q</sup>	N <sup>4</sup>	2 000	0.978	May - June	63	6	33	56	308	365	3 653
<i>M. macroura</i> <sup>q</sup>	N	1 500	0.620	April - June	60	4.5					
<i>Spilogale putorius</i> (W) <sup>r</sup>	Y	500	0.876	April - June	29	3.5					
<i>S. putorius</i> (E) <sup>r</sup>	N	430	0.833	May - Aug.	30	4.3	16	56		244	
<i>S. pygmaea</i> <sup>s</sup>	N	500	0.378	April - June	48						
<i>Conepatus mesoleucus</i> <sup>q</sup>	N	3 200	0.690	April - June	60	3.5					
<b>CANIDAE<sup>1</sup></b>											
<i>Canis lupus</i> <sup>t</sup>	N	31 100	1.149	March - May	63	5.5	425	135	913	365	5 387
<i>C. rufus</i> <sup>t</sup>	N	29 750	0.714		61	7			300	365	5 844
<i>C. latrans</i> <sup>u</sup>	N	9 700	0.881	March - May	62	6.2	225	98	365	365	6 575
<i>Urocyon cinereoargenteus</i> <sup>v</sup>	N	3 300	0.740	May - June	63	3.8	86		365	365	5 479
<i>U. littoralis</i> <sup>w</sup>	N	1 900	0.675	May	52	2.17			365	365	2 922
<i>Vulpes vulpes</i> <sup>x</sup>	N	3 900	1.184	March - May	55	4.8	105	56	313	365	4 383
<i>Alopex lagopus</i> <sup>y</sup>	N	2 900	1.507	March - April	54	7.1	66	43	293	365	3 287
<i>Vulpes macrotis</i> <sup>z</sup>	N	2 000	0.810	Feb. - March	52	4	40	30	660	365	4 383
<i>V. velox</i> <sup>aa</sup>	N	2 300	1.031	March - April	51	4.5		30	300	365	4 657
<b>FELIDAE<sup>1</sup></b>											
<i>Lynx canadensis</i> <sup>ab,ac</sup>	N	9 100	1.203	May - June	68	3.5	289	112	690	365	4 931
<i>L. rufus</i> <sup>ad</sup>	N	5 200	0.898	March - July	63	3.2	312	60	593	365	4 748
<i>Panthera onca</i> <sup>ae</sup>	N	67 000	0.600	all year	101	2	800	166	3103	365	8 036
<i>Herpailurus yagouaroundi</i> <sup>af,ag</sup>	N	6 750	0.684	all year	74	3					3 835
<i>Puma concolor</i> <sup>ah</sup>	N	39 600	0.882	all year	90	2.5	400	60	913	578	7 122
<i>Leopardus pardalis</i> <sup>af,ag</sup>	N	8 750	0.600	all year	75	1.4			35		6 696
<i>L. wiedii</i> <sup>af,ag</sup>	N	3 000	0.613		70	1.5		63	72		4 809

<sup>1</sup> Data from Gittleman (1986) complemented by: a, Stirling (1988), b, Pasitschniak-Arts (1993), c, Kolenosky & Strathern (1987), d, Nowak (1991), e, Poglayen-Neuwall & Towell (1988), f, Gompper (1995), g, Sanderson (1987), h, Clark *et al.* (1987), i, Powell (1981), j, Sheffield & King (1994), k, Fagerstone (1987), l, Dunstone (1993), m, Melquist & Dronkert (1987), n, Garshelis (1987), o, Pasitschniak-Arts & Larivière (1995), p, Messick (1987), q, Rosatte (1987), r, Mead (1989), s, Teska, Rybak & Baker (1981), t, Carbyn (1987), u, Bekoff (1977), v, Fritzell & Haroldson (1982), w, Moore & Collins (1995), x, Larivière & Pasitschniak-Arts (1996), y, Garrott & Eberhardt (1987), z, O'Farrell (1987), aa, Scott-Brown, Herrero & Reynolds (1987), ab, Tumilson (1987), ac, Bailey *et al.* (1986), ad, Rolley (1987), ae, Seymour (1989), af, Tewes & Schmidly (1987), ag, Jones (1977), ah, Lindzey (1987).

<sup>2</sup> Data for the Odobenidae, Phocidae, and Otariidae, from Reidman (1990), King (1983), and Kovacs & Lavigne (1986, 1992).

<sup>3</sup> Data from Mead (1989) unless specified otherwise.

<sup>4</sup> Both *Mustela vison* and *Mephitis mephitis* were listed as not having DI based on the short duration and high variability of the duration of delay: 0-37 and 0-14 days for *M. vison* and *M. mephitis*, respectively (Mead, 1981).