

Can comparing life histories help conserve carnivores?

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Abstract

The demographic relationship between life-history variation and environment may form a foundation for developing conservation strategy. We predicted that grouping 52 North American carnivore species based on life-history modules (reproductive output and reproductive chronology) would highlight differences in adaptations to particular environments. We tested whether differences among life histories related to particular environments classified according to primary productivity and seasonality into a 2 × 2 table. We found that bet-hedgers (e.g., bears, martens, fishers) have evolved life history adaptations to unpredictable environments, marine carnivores (e.g., seals) have evolved highly competitive abilities, and other terrestrial carnivores show adaptations to high reproduction (e.g., neotropical felids and procyonids) or survival (e.g., foxes and skunks). For example, ‘reproducers’ lived in environments with low seasonality and high primary productivity and were characterized by high reproductive output (long gestation, large neonates and small litters), short chronology of reproductive events (early age at maturity and short life), small home ranges and high population density. Conservation measures to promote carnivore populations should differ relative to the type of life history, emphasizing adult survival for bet-hedgers and survivors, and juvenile survival for reproducers and competitors.

INTRODUCTION

Development of conservation strategies for vertebrates can be built upon the strong pattern of covariation in life history (Sæther, 1988; Harvey, Read & Promislow, 1989; Shine & Charnov, 1992) and knowledge of the environmental selection pressures that shape life-history strategies (e.g., Gittleman, 1994). Relating life-history variation to environmental predictability and population processes may provide insights into species-specific conservation. For example, species with ‘slow’ life histories (i.e., late maturity, slow growth and low reproduction) require large areas and live at low densities in more unpredictable environments (Woodroffe & Ginsberg, 1998). As a result, these species are more susceptible to exploitation of adults than related species with ‘faster’ life histories (MacArthur & Wilson, 1967).

Here, we test the hypothesis that life histories group according to differences in environment and population processes (Sibly & Calow, 1985; Saether, Ringsby &

Roskaft, 1996; Ferguson & McLoughlin, 2000) and thus require different conservation approaches (e.g., Purvis *et al.*, 2000). First, we consider the major environmental selection pressures on life-history evolution as the amount of energy and variation in energy (Stevens, 1989; Tuljapurkar, 1990; Rosenzweig & Abramsky, 1993; Brown, 1995). The amount of energy in an environment can be measured as primary productivity (actual evapotranspiration) and variation can be measured as seasonality (Boyce, 1979; Zeveloff & Boyce, 1989). Although variation can also be measured at inter-annual scales (Ferguson *et al.*, 1999) we use seasonality (coefficient of variation among primary productivity calculated for 12 months) as a surrogate of variation (e.g., Zeveloff & Boyce, 1988; Ferguson & McLoughlin, 2000) as both seasonality and inter-annual variation are correlated with latitude (Slobodkin & Sanders, 1969; Ferguson & Messier, 1996).

Second, we group life-history traits into those associated with reproductive output and those associated with timing of reproduction. These two modules of life-history traits are probably linked by related trade-offs (Ferguson, Virgil & Larivière, 1996). Traits of reproductive output

include gestation length, neonate size and litter size, whereas traits related to reproductive chronology include age at maturity, interbirth interval and longevity. Also, we consider density, home-range size, sexual dimorphism and mating systems as important behavioural traits that may have conservation implications (Gittleman, 1993; Smallwood, 1999; Purvis *et al.*, 2000).

Next, we compare these two life-history modules and the two environmental selection pressures to make four predictions (Fig. 1). First, one group of animals consists of 'reproducers', which live in high-energy environments with low variation in energy (e.g., seasonality). Here, evolution selected for large reproductive output (long gestation, large neonates, small litter size) and a short chronology of reproductive events (early age at maturity, short inter-birth interval and short life). Second, 'competitors', are adapted to high-energy environments with high variability in the temporal and spatial distribution of energy. Competitor species are also characterized by a large reproductive output, but, in contrast, spread out reproductive events (delayed maturation and long life). Third, opposite to the reproducers on the slow-fast continuum are 'bet-hedgers' that live in low-energy environments with high seasonality. Bet-hedgers have evolved a strategy of low reproductive output (short gestation, many small neonates) with a greater chronological spread of reproductive events (Stearns & Crandall, 1981; Philippi & Seger, 1989). A fourth group, called 'survivors', are adapted to low primary productivity environments with low environmental variation, which has selected for species characterized by low

reproductive output and a shorter chronology of reproductive events.

We tested this model by first using the method of independent contrasts to investigate relationships between environmental (primary productivity and seasonality) and life-history variables. Second, we grouped variation in life history for North American carnivores and tested whether differences among groups related to particular environments. We predicted that grouping carnivores based on life history would highlight differences in adaptations to particular environments represented by the surrogate measures of energy and variation. Environments differ in available resources for reproductive production and in mortality pressure, and hence species adapted to these environments require different conservation strategies.

MATERIAL AND METHODS

Phylogeny and data

We used the phylogenetic tree proposed by Bininda-Emonds, Gittleman & Purvis (1999) and the taxonomy of Wozencraft (1993) except for two changes. First, we considered skunks a monophyletic clade, the family Mephitidae, separate from mustelids as recognized by the American Society of Mammalogists (Dragoo & Honeycutt, 1997). Second, we considered three species of spotted skunks (*Spilogale*): western spotted skunk (*S. gracilis*), eastern spotted skunk (*S. putorius*) and pygmy spotted skunk (*S. pygmaea*). The data consisted of nine families, 30 genera and 52 species of North American carnivores and life-history and behavioural traits were obtained from published sources (e.g., *Mammalian Species* articles; Hayssen, Tienhoven & Tienhoven, 1993; Silva & Downing, 1995; Ferguson *et al.*, 1996; Bininda-Emonds, 1998; Appendix 1). Gestation length does not include the period of delayed implantation.

Measures of primary productivity and seasonality were calculated as the sum and the coefficient of variation (CV) of monthly ($n = 12$) values of actual evapotranspiration respectively. Actual evapotranspiration is highly correlated with primary productivity (Rosenzweig, 1968). We estimated primary productivity ($g/m^2/y$) from actual evapotranspiration rates using a power function (Leith, 1976; Ferguson & McLoughlin, 2000). The mean and CV values were calculated for all weather stations ($n = 112$ across North America) within the historical geographic range of each carnivore species (Ferguson *et al.*, 1996). Larger actual primary productivity values indicated greater energy within a species' geographic range. Similarly, larger CV values indicated greater seasonality within the range of a species (Zevloff & Boyce, 1988). For marine carnivores we used data from coastal weather stations adjacent to marine distribution. However, cold-water environments inhabited by pinnipeds are considered the most productive marine environments in the world (Arrigo *et al.*, 1997; Nicol & Allison, 1997; Smith, Baker & Stammerjohn, 1998), and therefore we use pinnipeds to

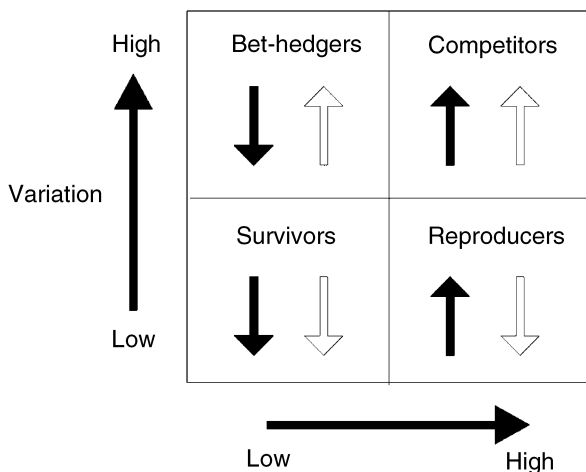


Fig. 1. Classification of life histories based on two major environmental selection pressures: energy (primary productivity) and variation (seasonality). First arrow ($\uparrow\downarrow$) indicates reproductive output (\uparrow = long gestation, large neonates, small litter size; \downarrow = short gestation, small neonates, large litter size). Second arrow ($\uparrow\downarrow$) indicates timing of reproductive events (\uparrow = late age at maturity, long interbirth interval, long life; \downarrow = early age at maturity, short interbirth interval, short life). For example, 'bet-hedgers' live in low primary productivity and highly variable environments and are predicted to reduce reproductive output but spread out the number of reproductive events.

represent species adapted to high primary productivity and high seasonal environments.

Mating systems are often coded as categorical data although the information can also be interpreted as coarse information on an underlying continuous variable (Garland *et al.*, 1993). Polygyny, promiscuity (multi-male mating) and monogamy can be considered groupings along a continuum from breeding group size greater than five for highly polygynous species, to breeding group size between three and five for weakly polygynous species associated with multi-male mating systems, to breeding group size of one or two for monogamous species (Clutton-Brock, Albon & Harvey, 1980; but see Gittleman & Van Valkenburgh, 1997). Hence, we scored the mating system data as three category-ordered variables: 3 = polygyny, 2 = multi-male, 1 = monogamy. We used female mass as a covariate to control for the effect of body size on sexual size dimorphism and thus mating system (Loison *et al.*, 1999).

Relationship between life history and environment

To test the hypothesis that life-history traits were related to environmental factors, we derived partial correlation coefficients using multiple regressions of phylogenetic independent contrasts (Felsenstein, 1985; PDTREE program of Garland, Midford & Ives, 1999). We tested the assumption that continuous traits evolve in a random-walk process by regressing the absolute values of the standardized contrasts against their standard deviations (square roots of sums of branch lengths; Garland *et al.*, 1993) and did not find significant correlations. We used partial correlation analysis of independent contrasts to determine if environmental factors explained variation in the following life-history traits: gestation length, neonate mass, litter size, longevity, nursing duration, age at maturity and interbirth interval. The independent variables included the same seven life-history traits, seasonality and primary productivity. We used stepwise selection (PROC REG; SAS, 1990) with entry and exit criteria and model acceptance set at $P < 0.05$. Normality of the contrast data was tested with Shapiro–Wilk test and all variables were normally distributed ($P > 0.35$).

Grouping carnivores

We grouped 52 North American carnivores using two cluster analyses (PROC CLUST; SAS, 1990) based on: (1) seven life-history traits (gestation length, neonate mass, litter size, period of lactation, age at maturity, interbirth interval and longevity); (2) three life-history traits (gestation length, age at maturity and litter size). The latter cluster analysis was considered necessary as only 37 carnivores had all seven life-history traits values used for the first cluster analysis. Canonical discriminant analysis (see below) indicated that gestation length, neonate mass, litter size and age at maturity contributed most to variation among groups of species. However, gestation length and neonate mass are highly

correlated ($r = 0.97$) and therefore we chose to restrict our second cluster analysis to using three traits.

Life-history traits were \log_{10} transformed prior to analyses and regressed against female body mass using least-squares linear regression. The residuals from that analysis were used in cluster analysis to control for body mass. Classification of species into groups was done by the average-linkage clustering method (Romesburg, 1984) using Euclidean distance as the similarity index with all variables standardized between 0 and 1. We also used canonical discriminant analysis to obtain a secondary validation of the classification of species. We did not use behavioural and environmental characteristics as variables in the clustering method as we wanted to use them to test our predictions.

Comparing groups to environments

We tested the assumption of statistical dependence in the data due to phylogeny that is the justification for using phylogenetic corrections (e.g., independent contrasts or simulations) and which may be restrictive (Ricklefs & Starck, 1996; Bjorklund, 1997). We tested for the hierarchical pattern of variation in life-history and behavioural traits using nested analysis of variance (PROC NESTED; SAS, 1990) at four phylogenetic levels of the carnivore tree divided into 13.45 million year time slices (see Bininda-Emonds & Gittleman, 2000). Almost identical results (not shown) were obtained using a nested analysis of variance of taxonomy (family, genus, species); not surprising as major taxonomic subdivisions generally coincide with time intervals (Harvey & Pagel, 1991). If most of the variation in traits occurs at higher phylogenetic levels (TS1–3) then we assumed that statistical dependence in the data due to phylogeny occurred and the data required phylogenetic correction. Conversely, if most of the variation occurred at the species level (TS4) then phylogenetic correction was not necessary. Here we assume that species values can be considered independent of phylogeny, although we recognize the limitations of our restrictive sample of North American carnivores.

We tested the prediction that carnivore groups have different life-history and behavioural traits related to environmental selection pressures (amount of energy and variation). We used Monte Carlo simulations of continuous traits along a phylogenetic structure (i.e., phylogenetic tree of 52 species that included four polytomies; Bininda-Emonds *et al.*, 1999) to estimate statistical parameters for phylogenetic analysis of covariance (ANCOVA; Garland *et al.*, 1993). Initial values corresponding to life-history 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 ($n = 1000$), we calculated phylogenetically corrected estimates of analysis of covariance parameters using general linear models.

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 enabled us to assess differences in traits due to groups alone (i.e., variation in body mass was statistically removed from the analysis). The adjusted trait values, or least-squared means, represented 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 (competitors, bet-hedgers, reproducers, survivors) was set at $\alpha = 0.05$ from the 95th percentile of the simulated distribution. We report significant differences in least-squared means that control for body size variation using Scheffe's multiple comparison method.

RESULTS

Four of the seven life history independent contrasts (corrected for body size and phylogeny) were correlated with environmental variables, and seasonality was common to all of these relationships (Table 1). The contrasts not correlated with environment were gestation length, longevity and age at maturity. Longer gestation length was related to smaller litters and larger offspring size. Longevity and age at maturity were positively related.

The life-history traits correlated with environment included: neonate mass, litter size, nursing duration and interbirth interval. Environments characterized by greater seasonality were associated with larger neonates, larger litters, longer nursing duration and longer interbirth intervals. Evidence for an interaction between primary productivity and seasonality is indicated by a negative correlation between the variables ($r = -0.53$, $P = 0.0006$, $n = 52$), yet both were positively related to neonate mass and litter size. Hence, litter size and neonate size may have increased in northern areas with

increasing seasonality, and increased in southern areas with greater primary productivity.

Next, we grouped carnivores according to life histories. The first cluster analysis based on seven life-history traits indicated five groups of carnivores. However, owing to small numbers of species with information on all seven traits ($n = 37$) we reran the cluster analysis using only three traits (gestation length, age at maturity and litter size) and obtained a sixth group of carnivores (F; Fig. 2) as well as inclusion of carnivores with some missing information into the clusters defined from seven life-history traits. Species that remained as outliers and not used in the subsequent analyses were *Mustela erminea* (late age at maturity), *Mustela nivalis* (long gestation), *Enhydra lutris* (small litter size), *Spilogale pygmaea* (long gestation) and *Mirounga angustirostris* (short gestation).

Confirmation of the grouping was obtained using discriminant analysis with significant differences among the six clusters (Wilk's λ , $P < 0.001$). The first discriminant function (linear combination of variables) explained 67% of the variation among species and was positively correlated with gestation period ($r = 0.98$) and neonate mass ($r = 0.87$). The second discriminant function explained 30% of the variation and was correlated with litter size ($r = 0.84$) and age at maturity ($r = -0.73$).

Group A included northern canids ($n = 4$) that were characterized by large litters, large home ranges and low density (Table 2). This group was most distinct according to the cluster analysis and includes cooperative breeders that allow breeding females to have high reproduction, whereas the mean reproductive rate across individuals is rather low owing to suppressed reproduction of group members. Group B included three northern felids, four mustelids, raccoon (*Procyon lotor*) and eastern spotted skunk (*Spilogale putorius*) that were average in all traits. Group C included five foxes, badger (*Taxidea taxus*) and four skunks that were characterized by small neonates, short lactation period,

Table 1. Partial correlation analysis to determine correlates of life-history and environmental factors using independent contrasts for 52 species of North American carnivores

Life-history trait	Dependent variables				
	<i>F</i>	<i>P</i>	Sign	Variable	Partial <i>R</i> ²
Gestation length	11.9	0.0003	-	Litter size	0.128
			+	Neonate mass	0.370
Neonate mass	15.6	0.0001	+	Female mass	0.396
			+	Gestation	0.187
			+	Energy ^a	0.103
			+	Seasonality ^b	0.053
			+	Energy	0.110
Litter size	3.93	0.017	+	Seasonality	0.101
			+	Maturity	0.270
Longevity	8.9	0.007	+		
Nursing duration	6.5	0.006	-	Litter size	0.224
			+	Seasonality	0.138
Age at maturity	10.2	0.0007	+	Longevity	0.270
			+	Female mass	0.200
Interbirth interval	8.5	0.0006	+	Female mass	0.301
			+	Seasonality	0.152
			+	Longevity	0.082

^a energy calculated as primary productivity

^b seasonality calculated as coefficient of variation of 12 measures of actual evapotranspiration for each month of the year

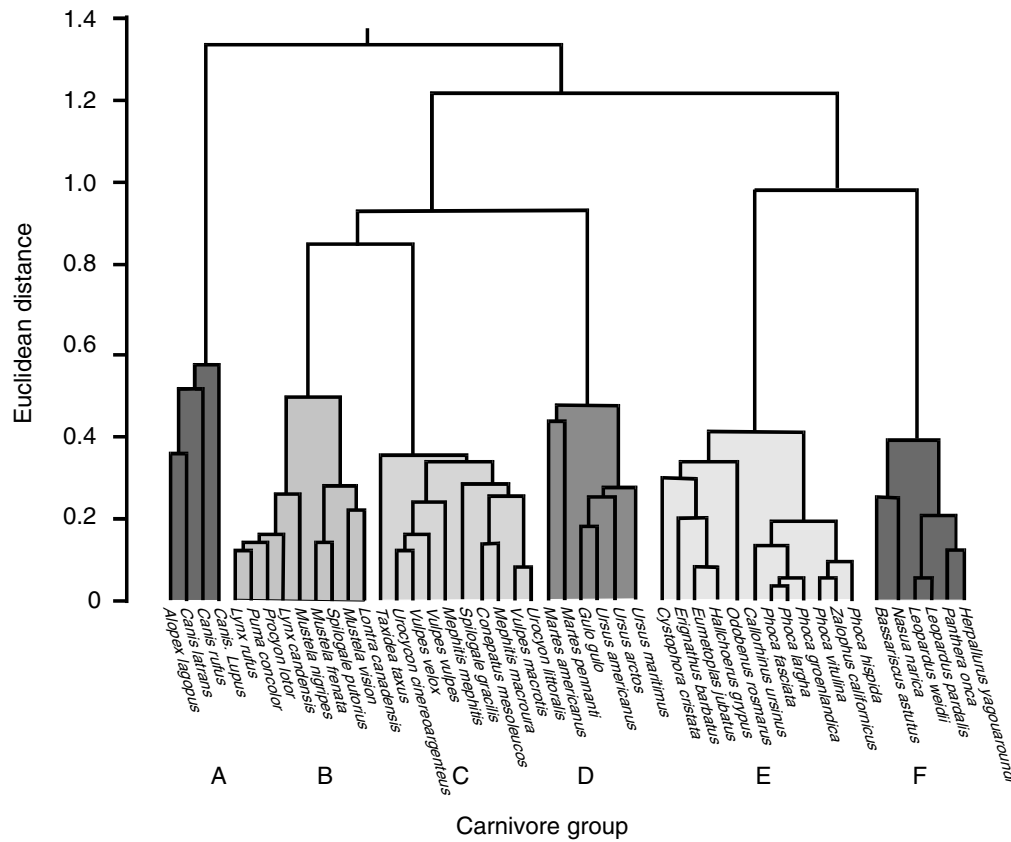


Fig. 2. Dendrogram of North American carnivore species grouped according to a cluster analysis based on life-history traits. Groups are as follows: A and E, competitors; B and F, reproducers; C, survivors; and D, bet-hedgers.

Table 2. Summary statistics of traits uncorrected for body size and phylogeny for six groups of North American carnivore species identified using cluster analysis

Life-history traits:							
Group	Gestation length (d)	Neonate mass (g)	Litter size	Weaning duration (d)	Age at maturity (d)	Interbirth interval (d)	Longevity (d)
A	60.0 ± 2.0	238.7 ± 103.9	6.45 ± 0.38	92.0 ± 26.7	476.8 ± 149.3	365.0 ± 0.0	5273 ± 706
B	52.8 ± 7.4	159.4 ± 54.9	3.59 ± 0.21	69.9 ± 12.4	532.0 ± 73.6	375.2 ± 28.6	4337 ± 503
C	52.7 ± 3.3	71.6 ± 14.7	4.08 ± 0.31	49.7 ± 8.3	357.3 ± 50.5	365.0 ± 0.0	4318 ± 310
D	47.8 ± 7.8	263.7 ± 106.1	2.42 ± 0.15	308.3 ± 140.9	1105 ± 251	669.7 ± 99.2	7295 ± 1346
E	251.0 ± 7.4	17575 ± 4633	1.00 ± 0.00	131.9 ± 58.9	1551.5 ± 99.2	502.1 ± 81.5	11821 ± 902
F	75.0 ± 6.6	273.8 ± 137.4	2.23 ± 0.45	94.0 ± 19.2	775.0 ± 140.0	365.0 ± 0.0	5418 ± 779
Mean	106.2 ± 12.8	5543 ± 1899	2.95 ± 0.25	125.9 ± 29.4	878.2 ± 86.4	446.0 ± 30.2	6960 ± 579

Environmental, behavioural and demographic traits:					
Group	Primary productivity ($g\ m^{-2}\ y^{-1}$)	Seasonality (CV)	Male home-range size (km^2)	Female home-range size (km^2)	Density (km^{-2})
A	1094 ± 229	1.063 ± 0.173	211.7 ± 175.4	178.6 ± 128.3	0.23 ± 0.22
B	1121 ± 59	1.002 ± 0.046	86.6 ± 49.4	56.2 ± 40.1	5.17 ± 2.48
C	953 ± 62	0.853 ± 0.057	7.0 ± 1.84	5.4 ± 1.9	3.25 ± 1.43
D	920 ± 50	1.193 ± 0.068	279.0 ± 137.1	129.1 ± 70.4	0.33 ± 0.25
E	803 ± 51	1.272 ± 0.079	–	–	1.22 ± 0.77
F	1231 ± 86	0.659 ± 0.030	24.2 ± 11.1	9.0 ± 4.0	7.38 ± 6.43
Mean	990 ± 36	1.025 ± 0.042	100.6 ± 35.0	65.3 ± 24.8	3.26 ± 1.13

early age at maturity, short life and small home-range size. Group D included all three bears, and three mustelids that were characterized by short gestation, long period of lactation, long interbirth interval and large home range size. Group E included 12 pinnipeds that were characterized by long gestation, large neonates, small litter size, late age at maturity and long life. Group

F included neotropical cats ($n = 4$) and two neotropical procyonids (ringtail, *Bassariscus astutus*, and coati, *Nasua narica*) that were characterized by high density and that live in areas of highest primary productivity and lowest seasonality.

Next, we tested if differences in trait values (reproductive output and chronology of reproductive events)

among carnivore groups matched our predictions related to particular environments (energy and variation) according to a 2×2 table (Fig. 1). We plotted group means for energy (primary productivity) and variation (seasonality) (Fig. 3) and chose four extreme groups that might match our classification. Pinnipeds (group E) were chosen to represent competitors, assuming that they lived in a marine environment of greater primary productivity (see Methods). We considered group D (three bears and three mustelids) to represent bet-hedgers; group F (neotropical cats and procyonids) to represent reproducers; and group C (foxes and skunks) to represent survivors.

Nested analysis of variance revealed that variation in life-history data was greater at the higher phylogenetic level (TS1-3) for all life-history traits (gestation length, neonate mass, litter size, longevity, nursing duration, age at maturity, sexual dimorphism and interbirth interval; Table 3). Thus, using phylogenetic correction methods, we found differences between the four groups of carnivores for gestation length, neonate mass, litter size, age at maturity and longevity (Table 4). As predicted, competitors (group E) and reproducers (group F) had relatively greater reproductive output (long gestation length, large neonate mass and small litters), whereas bet-hedgers (group D) and survivors (Group C) had relatively less reproductive output (short gestation length, small neonate mass and large litters). As predicted, survivors and reproducers had a shorter chronology of reproductive events characterized by early age at maturity (survivors) and/or short life (survivors and reproducers). In contrast, bet-hedgers and competitors had a greater temporal chronology of reproductive events as indicated by late maturity (bet-hedgers) and long life (competitors; Table 4).

In contrast to life-history traits, the pattern of variation

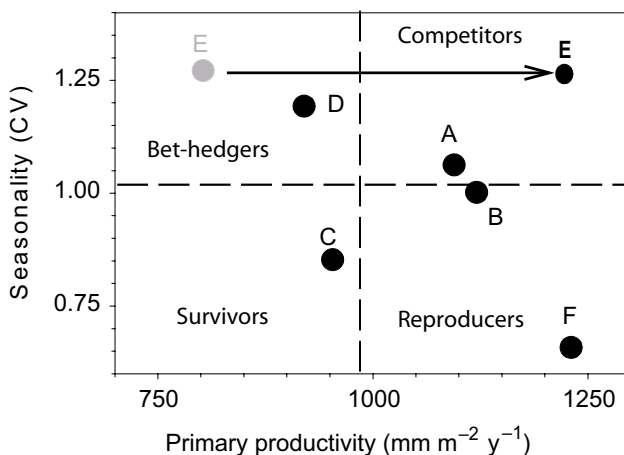


Fig. 3. Relationship between energy (primary productivity) and variation (seasonality) for six groups of North American carnivores. Groups are as follows: A and E, competitors; B and F, reproducers; C, survivors; and D, bet-hedgers. Dashed lines represent means. Group E are thought to live in high-energy environments (arrow) as methods used to estimate primary productivity of marine environments underestimated true marine primary productivity (see Methods).

Table 3. Comparison of relative variance (nested analysis of variance) attributable to five time slices at intervals of 13.45 million years (taxa with 2, 3, 6, 16 and 52 members for TS1 to TS4) of eight life-history and seven behaviour traits for species of North American carnivores.

Trait	Percent of total variance			
	TS1	TS2	TS3	TS4
Life-history behaviour				
environmental				
Gestation length	0.0	92.0	4.1	3.9
Neonate mass	0.0	86.9	6.9	6.2
Mating system	67.0	2.4	21.2	9.4
Litter size	0.0	82.6	1.7	15.7
Nursing duration	0.0	17.1	64.8	18.0
Longevity	0.0	80.2	1.1	18.7
Age at maturity	0.0	75.5	0.1	24.5
Sexual dimorphism	1.9	0.0	64.0	34.1
Interbirth interval	0.0	41.9	18.3	39.8
Male home range	0.0	41.2	16.6	42.2
Female home range	0.0	47.4	0.0	52.6
Primary productivity	8.6	0.0	36.4	55.0
Seasonality	0.0	4.9	25.6	69.5
Population density	5.3	15.1	0.0	79.6

for behavioural traits (male and female home-range size, and population density) showed greater variance at the species level (TS4; Table 3). Differences among groups were detected for male and female home-range size and population density (Table 5). Survivors and reproducers had smaller home ranges and higher density, whereas bet-hedgers had larger home ranges and lived at relatively lower density (Table 5).

DISCUSSION

Our results illustrate that North American carnivores can be grouped on the basis of life-history traits in relation to environmental gradients according to a 2×2 table that focuses conservation approaches (Fig. 1). Most (four of seven) life-history contrasts were correlated with energy and variation. As well, our results provide a simple quantitative basis for predicting vulnerability to habitat disturbance and linking life histories, environmental predictability and population dynamics. North American carnivores are greatly influenced by environmental energy and associated variation, with seasonal variation predominating over primary productivity (Zelveloff & Boyce, 1988).

For species living in the most stable environments (i.e., reproducers), conditions seldom change and animals can afford to invest in long gestation and few large neonates. Species such as neotropical cats and procyonids also display short longevity, which suggests that these populations are most influenced by fluctuations in juvenile survival. Therefore, conservation efforts should ensure reasonable juvenile survival and maintain relatively undisturbed environments. For example, deforestation that results in increased seasonal extremes of temperature and precipitation would adversely affect reproducers.

Competitors are adapted to high-energy environments with high variability in the temporal and spatial distribution of primary productivity. Competitors, such as pin-

Table 4. Results of analysis of covariance tests (ANCOVA) for difference between groups ($n = 6$) for North American carnivore species. The covariate is female body mass. Models of evolutionary change were no phylogenetic change (conventional ANCOVA) or gradual evolutionary change (proportional to branch lengths) according to results from Table 3.

Life-history and behaviour traits	Conventional ANCOVA				Least-squared means				Phylogenetic		
	Observed n	F	Critical F	P	Reproducers	Competitors	Bet-hedgers	Survivors	Mean	Critical F	P
Gestation length	34	203	2.89	0.0001	85	182	42	69	93	21.2	0.0001
Neonate mass	28	358	2.94	0.0001	457	4169	178	257	871	18.1	0.0001
Litter size	34	40.4	2.89	0.0001	1.9	1.1	2.4	3.7	2.0	23.9	0.001
Mating system	32	2.47	2.91	0.07	2.0	2.4	2.0	1.6	2.0	27.3	>0.20
Longevity	30	33.3	2.92	0.0001	6457	8128	6761	6026	6918	25.5	0.01
Nursing duration	29	3.75	2.93	0.02	162	22	186	110	68	26.0	>0.20
Age at maturity	31	50.9	2.91	0.0001	955	933	977	562	832	24.3	0.001
Sexual dimorphism	34	1.30	2.89	0.29	1.4	1.6	1.7	1.3	1.5	23.1	>0.20
Interbirth interval	31	8.68	2.91	0.0001 ^a	437	339	631	501	437	26.2	>0.20

^a Slope differs significantly between groups

Table 5. Results of analysis of covariance tests (ANCOVA) for trait differences among six groups of North American carnivore species ($n = 52$). 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) according to results from Table 3.

Environment and behaviour traits	ANCOVA			Least-squared mean				
	n	F	P	Reproducers	Competitors	Bet-hedgers	Survivors	Mean
Seasonality	34	12.0	0.0001	0.69	1.21	1.19	0.91	1.03
Primary productivity	34	5.5	0.002	1238	787	919	968	943
Female home range	18	14.3	0.0002	3.5	NA	57.8	8.6	12.6
Male home range	18	9.7	0.001	7.2	NA	64.4	7.8	13.7
Population density	17	5.9	0.009	0.93	NA	0.13	0.76	0.43

nipeds, invest considerably in annual reproduction (Kovacs & Lavigne, 1986, 1992; Ferguson *et al.*, 1996), as exemplified by their long gestation, large neonates and very small litter size ($n = 1$; Bininda-Emonds & Gittleman, 2000). However, the environmental variability warrants many reproductive events, as recruitment variability is high (Fowler, 1990; Boness & Bowen, 1996). Thus, competitors experience delayed maturation, but high adult survival and long life. Although our data were insufficient for testing, differences were not found in density and home-range size between pinnipeds and fissiped carnivores (Bininda-Emonds & Gittleman, 2000). Population persistence for K -selected competitors is more influenced by environmental changes affecting adult survival. Therefore, conservation efforts should maintain high adult survival while allowing individuals access to large areas that permit a space-use strategy that controls high environmental variability.

Opposite to the reproducers on the slow-fast continuum is a group of carnivores with high adult survival rates that we have called bet-hedgers. Our analyses revealed that bet-hedgers included all three North American bears (*Ursus americanus*, *U. arctos* and *U. maritimus*) as well as three forest-dwelling mustelids (*Martes americana*, *M. pennanti* and *Gulo gulo*). The reproductive output of bet-hedgers is determined by stochastic variation in birthing conditions, such as large annual fluctuations in food resources, climate or predation rate (Liou *et al.*, 1993). The mean reproductive output across years may be similar for reproducers and competitors; however, the variance among years in the

reproductive success will be larger among bet-hedgers relative to competitors (Lindström, 1999).

Conservation strategies for bet-hedgers should ensure high adult survival. For species harvested by trapping, such as American marten (*M. americana*) and fisher (*M. pennanti*), trapping of juveniles during the early autumn dispersal period is much more conservative than late-season trapping of resident adults (Quick, 1956). For polygynous bears, harvest should be directed towards males, whereas females should be protected whenever possible (Kolenosky, 1986). Among North American carnivores, bet-hedgers are the group most susceptible to overharvesting.

A fourth group, called survivors, lives in low primary productivity environments with little seasonal variation, like desert or prairie habitats. Low primary productivity environments generally support few carnivores (Oksanen *et al.*, 1981; Moen & Oksanen, 1991). Interestingly, all species of survivors are omnivores, which may facilitate survival in low primary productivity environments. In other taxa, such as reptiles and amphibians, generalist carnivores also occupy environments with low primary productivity and low seasonality (Pfrender, Bradshaw & Kleckner, 1998). Life-history characteristics of survivors include short gestation, small neonates, large litters, early age at maturity and short life. Conservation for survivors should include demographic efforts to improve juvenile survival and landscape management to maintain low energy and a more uniform distribution of seasonal energy. For example, irrigation and flooding of precipitation-limited

landscapes may indirectly harm survivors by improving demography of reproducers as potentially competing species.

Life-history variation results in different carnivore groups requiring specific conservation efforts to prevent population declines. In general, variation in adult versus juvenile survival rate can explain a high proportion of the differences in reproductive traits, leading to robust, often invariant, relationships between different life-history variables (Charnov, 1993; Gittleman, 1993, 1994; Flegr, 1997). For example, forest mustelids such as marten and fisher are highly susceptible to overexploitation (Ruggiero *et al.*, 1994; S. H. Ferguson & S. Larivière, unpublished data), whereas other species of North American carnivores may withstand high harvesting pressure (Berryman, 1972; King & Moors, 1979; Buskirk, 1999; Larivière, Jolicœur & Crête, 2000). Considering life histories before implementing conservation and exploitation strategies is already common practice in fisheries science (Bannerot, Fox & Powers, 1987; Trippel, 1995; Jennings, Reynolds & Mills, 1998) and bird conservation (Sæther *et al.*, 1996), and for carnivores, life histories are significantly related to extinction risk (Purvis *et al.*, 2000).

Effects of landscape modification from agriculture (e.g., fragmentation of prairie habitats) or forestry (e.g., fragmentation of rainforests) reduce the size and contiguity of remaining habitat patches (Wilcox & Murphy, 1985; Meyer & Turner, 1992). In these altered landscapes, the effect of harvesting depends on individual species' life histories, ranging from mild in the case of coyotes (*Canis latrans*) to severe for larger carnivores such as grizzly bears (*Ursus arctos*; Fuller & Kittredge, 1996). With increasing concern for the conservation status of many carnivores (Gittleman, 1994; Mech, 1996), it is important to assess their vulnerability to overharvesting and habitat loss (Fuller & Kittredge, 1996). Our analyses suggest that examination of a relatively simple component of life-history, such as environmental predictability, can indicate the response to human-mediated landscape disturbance, and may facilitate the development of some general principles that managers can use to direct conservation efforts.

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Appendix 1. Life-history, behaviour and environmental data for 52 species (nine families) of North American carnivores

Family species	Body mass males (g)	female (g)	Sexual dimorphism	Primary productivity (g/m ² /y)	Seasonality	Gestation (d)	Litter size	Neonate mass (g)	Lactation duration (d)	Age maturity (d)	Interbirth interval (d)	Longevity (d)	Mating	Oestrus length system	Home-range size male (km ²)	female (km ²)	Density (/km ²)
Ursidae																	
<i>Ursus americanus</i> ^a	76,650	54,050	1.42	1032.7	1.036	70	2.5	285	170	1834	822	8218	2	3	153	57	0.28
<i>U. arctos</i> ^b	200,000	118,670	1.69	835.9	1.119	63	2	500	724	1338	913	9253	2	3	723	377	0.023
<i>U. maritimus</i> ^c	550,000	225,000	2.44	733.3	1.513	62	1.9	642	776	1734	731	12,419	2	30	–	125,000	0.015
Odobenidae^d																	
<i>Odobenus rosmarus</i>	1,246,000	690,000	1.81	650.3	1.641	315	1	58,000	676	2008	1278	12,784	3	–	–	–	–
Phocidae^d																	
<i>Cystophora cristata</i>	300,000	160,000	1.88	1066.9	1.130	234	1	27,000	5	1095	365	9131	1	–	–	–	–
<i>Erignathus barbatus</i>	290,000	290,000	1.00	775.1	1.458	285	1	38,000	15	2008	731	11,323	2	–	–	–	–
<i>Halichoerus grypus</i>	388,000	175,000	2.22	1122.1	1.084	236	1	14,900	21	1460	365	16,802	3	–	–	–	–
<i>Mirounga angustirostris</i>	2,250,000	900,000	2.50	591.5	0.741	210	1	33,600	28	1460	365	7305	3	–	–	–	–
<i>Phoca fasciata</i>	74,000	74,000	1.00	660.1	1.480	234	1	9400	32	1278	365	10,958	2	–	–	–	–
<i>P. groenlandica</i>	130,000	130,000	1.00	867.4	1.428	267	1	10,000	12	1825	365	12,784	2	–	–	–	–
<i>P. hispida</i>	71,000	69,000	1.03	650.3	1.595	225	1	4100	50	1825	365	15,706	3	–	–	–	–
<i>P. largha</i>	97,000	86,000	1.13	644.1	1.519	248	1	8300	25	1278	365	12,784	3	–	–	–	–
<i>P. vitulina</i>	95,000	78,000	1.22	914.0	1.085	248	1	10,100	21	1278	365	12,784	2	–	–	–	–
Otaridae^d																	
<i>Callorhinus ursinus</i>	220,000	43,000	5.12	857.4	0.925	240	1	5200	110	1095	365	7670	3	–	–	–	–
<i>Eumetopias jubatus</i>	968,000	333,000	2.91	848.5	1.026	240	1	17,600	347	1825	731	–	3	–	–	–	–
<i>Zalophus californicus</i>	245,000	82,000	2.99	573.9	0.888	240	1	8300	269	1643	365	7305	3	–	–	–	–
Procyonidae																	
<i>Nasua narica</i> ^d	5900	3500	1.69	1157.5	0.663	74	4	140	89	1020	365	6209	2	–	0.65	0.65	33
<i>Procyon lotor</i> ^g	6760	5940	1.14	1217.0	1.162	65	3.8	106	120	540	365	3653	2	3.	8.71	2.87	7.86
<i>Bassariscus astutus</i> ^e	900	700	1.29	915.0	0.791	52	3	28	71	300	365	2922	2	2	0.434	0.203	3.2
Mustelidae																	
<i>Lontra canadensis</i> ⁱ	8760	7860	1.11	1044.8	1.089	62	3	140	93	730	365	4745	2	46	231	70	3.16
<i>Enhydra lutris</i> ^h	33,350	23,600	1.41	859.1	0.974	120	1	2100	363	1095	365	–	2	4	–	4.82	13.25
<i>Martes pennanti</i> ^l	4760	2390	1.99	1016.8	1.117	23	2.7	28	63	730	365	3653	2	8	38	15	0.124
<i>M. americana</i> ^k	860	565	1.52	1016.8	1.178	27	2.6	28	46	365	365	4566	2	–	15	4.5	1.55
<i>Mustela erminea</i> ^m	138	57	2.42	890.6	1.206	30	4.5	2	66	336	365	2557	2	28	0.225	0.125	8
<i>M. nigripes</i> ⁿ	1500	1350	1.11	942.1	0.969	44	3.5	–	–	315	365	4018	2	9	1.71	0.487	2
<i>M. frenata</i> ^a	305	165	1.85	1169.0	0.887	24	4.5	3	30	252	365	2557	2	4	0.70	0.79	10
<i>M. nivalis</i> ^o	75	53	1.42	986.7	1.204	42	5.8	3	32	90	183	1096	2	–	0.134	0.036	60
<i>M. vison</i> ^p	1523	852	1.79	1052.8	1.097	29	4	9	28	420	365	2922	2	21	5.12	2.77	0.4
<i>Gulo gulo</i> ^j	14,800	10,600	1.40	883.7	1.194	35	2.8	99	71	630	822	5661	2	–	466	192	0.0075
<i>Taxidea taxus</i> ^q	8400	6400	1.31	975.0	0.925	42	4	94	42	395	365	4748	2	–	5.8	2.4	0.71
Mephitidae																	
<i>Conepatus mesoleucus</i> ^r	2168	1152	1.88	1124.3	0.690	60	3.5	–	–	–	–	–	2	–	–	–	–
<i>Mephitis macroura</i> ^s	806	717	1.12	887.1	0.620	60	4.5	–	–	–	–	–	2	–	–	–	–
<i>M. mephitis</i> ^t	2820	2000	1.41	1074.5	0.978	63	6	33	56	308	365	3653	3	3	8.36	3.74	10.45
<i>Spilogale gracilis</i> ^r	483	397	1.22	695.8	0.876	29	3.5	–	–	152	365	–	2	–	–	–	–
<i>S. putorius</i> ^d	399	283	1.41	1495.4	0.833	30	4.3	16	56	335	244	–	2	–	–	–	22.5

Appendix 1. continued

Family species	Body mass		Sexual dimorphism	Primary productivity (g/m ² /y)	Seasonality	Gestation (d)	Litter size	Neonate mass (g)	Lactation duration (d)	Age maturity (d)	Interbirth interval (d)	Longevity (d)	Mating	Oestrus length system	Home-range size		Density (/km ²)
	males (g)	female (g)													male (km ²)	female (km ²)	
<i>S. pygmaea</i> ^a	230	–	–	1364.9	0.378	48	6	7	53	308	365		2	–	–	–	–
<i>Canidae</i>																	
<i>Alopex lagopus</i> ^a	3620	3220	1.12	676.8	1.507	54	7.1	66	43	293	365	3287	1	5	21.2	21.2	
<i>Canis latrans</i> ^a	16,750	13,620	1.23	1032.1	0.881	62	6.2	225	98	365	365	6575	1	10	51.8	51.8	0.45
<i>C. lupus</i> ^a	50,000	36,500	1.37	925.1	1.149	63	5.5	425	135	913	365	5387	1	9	562	562	0.014
<i>C. rufus</i> ^a	27,680	21,630	1.28	1743.7	0.714	61	7	–	–	300	365	5844	1	–	–	79.5	–
<i>Urocyon cinereoargenteus</i> ^c	3700	3500	1.06	1275.7	0.740	63	3.8	86	84	365	365	5479	1	–	2.23	2.09	0.606
<i>U. littoralis</i> ^{aa}	1950	1900	1.03	793.8	0.675	52	2.2	–	–	365	365	2922	1	–	0.412	0.412	3.45
<i>Vulpes macrotis</i> ^{ab}	2200	1900	1.16	647.1	0.810	52	4	40	30	660	365	4383	1	–	7.53	7.53	0.221
<i>V. vulpes</i> ^{ad}	4100	3400	1.21	1028.6	1.184	55	4.8	105	56	313	365	4383	1	3	15.1	15.1	1.35
<i>V. velox</i> ^{ac}	2440	2250	1.08	1049.4	1.031	51	4.5	–	30	300	365	4657	1	–	9.6	6.63	5.94
<i>Felidae</i>																	
<i>Lynx canadensis</i> ^{ah}	9870	8430	1.17	888.4	1.203	68	3.5	289	112	690	365	4931	2	2	19.5	17.3	0.047
<i>L. rufus</i> ^{ai}	9600	6800	1.41	1128.5	0.898	63	3.2	312	60	593	365	4748	2	44	52.4	24.4	0.135
<i>Puma concolor</i> ^{ak}	60,000	40,000	1.50	1147.2	0.882	90	2.5	400	60	913	578	7122	2	8	374	331	0.462
<i>Herpailurus yagouaroundi</i> ^{al}	5600	4500	1.24	1172.1	0.684	67	2	–	–	–	–	3835	2	3	68.6	18.9	0.388
<i>Panthera onca</i> ^{aj}	94,900	67,000	1.42	1207.3	0.600	101	2	800	166	3103	365	8036	2	7	44.7	17.5	0.135
<i>Leopardus pardalis</i> ^{af}	11,200	7800	1.44	1449.1	0.600	75	1.4	276	90	730	365	6696	2	7	17.3	7.93	0.195
<i>L. wiedii</i> ^{ag}	3600	3000	1.20	1482.1	0.613	81	1	125	54	730	365	4809	2	10	13.4	–	–

^a Larivière (2000); ^b Pasitschniak-Arts (1993); Ferguson & McLoughlin (2000); ^c DeMaster & Stirling (1981); Ferguson *et al.* (1999); ^d Bonner (1990); King (1983); Kovacs & Lavigne (1986, 1992); ^e Poglajen-Neuwall & Towell (1988); ^f Gompper (1995); ^g Llewellyn & Enders (1954); Lotze & Anderson (1979); ^h Garshelis (1987); ⁱ Pasitschniak-Arts & Larivière (1995); Mead *et al.* (1993); ^j Larivière & Walton (1998); ^k Clark *et al.* (1987); ^l Powell (1993); ^m Fagerstone (1987); ⁿ Sheffield & Thomas (1997); ^o Sheffield & King (1994); ^p Larivière (1999); ^q Messick (1987); ^r Patton (1974); ^s Armstrong, Jones & Birney (1972); ^t Verts (1967); Wade-Smith & Richmond (1978); ^u Kinlaw (1995); Greensides & Mead (1973); ^v Testa, Rybak & Baker (1981); ^w Anthony (1997); ^x Voigt & Berg (1987); ^y Carbyn (1987); ^z Paradiso & Nowak (1972); ^{aa} Fritzell & Haroldson (1982); ^{ab} Moore & Collins (1995); ^{ac} McGrew (1979); ^{ad} Egoscue (1979); ^{ae} Larivière & Pasitschniak-Arts (1996); ^{af} Oliveira (1998a); ^{ag} Richard-Hansen *et al.* (1999); ^{ah} Oliveira (1998b); ^{ai} Quinn & Parker (1987); ^{aj} Larivière & Walton (1997); ^{ak} Seymour (1989); ^{al} Lindzey (1987). Sexual size dimorphism = male mass/female mass. Mating systems include: 1 = monogamy; 2 = promiscuity (multi-male); and 3 = polygyny.