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Correlates of speciation and extinction rates in the Carnivora

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ABSTRACT

Despite great research interest in macroevolutionary patterns in mammals, the factors causing differences in diversity among carnivoran lineages remain unclear. In this study, I analyse whether differences in body size, degree of trophic specialization and sociality level among carnivoran lineages are associated with differences in speciation and/or extinction rates during their recent evolutionary history (Miocene to Recent). I control for the effects of phylogenetic non-independence and use data on the diversity of both fossil and extant taxa to estimate extinction and speciation rates. The results, albeit based on a small sample size, indicate that lineages of highly social carnivorans have significantly higher extinction rates than carnivoran lineages that live solitarily or in small family groups. The results also indicate that the effect of sociality on extinction rates is independent of the effects of body size and trophic specialization. This pattern is explained by the combined effect of intense intra-guild competition, the Allee effect and the relatively small effective population sizes in carnivoran lineages that display reproductive suppression.

Keywords: Allee effect, Carnivora, competition, extinction, reproductive suppression, sociality, speciation.

INTRODUCTION

Identifying the factors that make taxa more or less prone to speciation and/or extinction is not only important for understanding evolutionary and ecological patterns, but also for defining and implementing conservation plans and priorities. Accordingly, phylogenetic patterns associated with differences in phenotypic and ecological traits have been analysed for several animal groups and geological times. Traits often cited as affecting speciation and extinction probabilities include body size, genetic variability, population density, degree of habitat or trophic specialization, dispersal abilities, rates of reproduction, life-history traits and geographic distribution (Vrba, 1984, 1989; Jablonski, 1986, 1987, 1994; Lewin, 1986; Raup, 1986, 1992; Stanley, 1986, 1991; Owen-Smith, 1987; Pimm *et al.*, 1988; Raup and Boyajian, 1988; Dial and Marzluff, 1989; Marzluff and Dial, 1991; Barraclough *et al.*, 1998; Gittleman and Purvis, 1998; Smith and Jeffrey, 1998; Purvis *et al.*, 2000). Despite great

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research interest in these issues, few studies have focused on correlates of speciation and extinction rates in mammals (Vrba, 1984, 1989; Martin, 1992; Gittleman and Purvis, 1998), and only one has concentrated on carnivores (Gittleman and Purvis, 1998). Gittleman and Purvis (1998) tested the association between differences in body size and species richness in extant Carnivora and Primates, but their results did not indicate a clear pattern. Thus, the factors causing differences in speciation and extinction rates among carnivoran lineages remain unclear (Gittleman and Purvis, 1998).

In this paper, I explore the effect that differences in body size, trophic specialization and sociality level have on speciation and extinction rates during the recent evolutionary history (Miocene to the Present) of four carnivoran groups: Caninae, Ursinae, Felinae and Hyaenidae. I control for the effects of phylogenetic non-independence and use data from the known fossil record and the diversity of extant species to estimate extinction and speciation rates.

I test the null hypothesis that differences in speciation and extinction rates among carnivoran lineages are not significantly different from random variation. Alternatively, it is expected that lineages of small-bodied carnivorans have higher speciation rates than lineages of larger ones. The reason is that small body size is associated with high reproductive rates and short life histories (Vrba, 1989), leading to increased rates of introduction of variation into populations of small mammals. This, in turn, results in higher rates of speciation and/or phyletic evolution in clades of small mammals compared with clades of larger ones (Vrba, 1989; Brooks and McLennan, 1991; Marzluff and Dial, 1991; Jablonski, 1996; Lessa and Farina, 1996; Lessa *et al.*, 1997). In addition, small-sized organisms are expected to have lower extinction rates because they require less energy to survive than their larger relatives during periods of environmental stress (Schmidt-Nielsen, 1984; Brooks and McLennan, 1991).

On the other hand, clades of large carnivorans are expected to be prone to extinction. Besides having slow life-history traits, large-bodied mammals tend to live at low population densities, and this makes them more vulnerable to environmental perturbations and more prone to extinction compared with clades of small mammals (Owen-Smith, 1987; Raup and Boyajian, 1988; Raup, 1992; Jablonski, 1996; Lessa and Farina, 1996; Purvis *et al.*, 2000). After an event of increased mortality, the balance between fecundity and mortality rates is offset, and populations of large mammals will be forced to remain for long periods at very low densities. For this reason, they become more susceptible to the effects of inbreeding, genetic drift, and demographic and environmental stochasticity (Pimm *et al.*, 1988; Lande, 1993; Bennett and Owens, 1997; Purvis *et al.*, 2000). In contrast, it has been hypothesized (Pimm, 1991; Lawton, 1994) that large-bodied vertebrates are less susceptible to environmental perturbation and, therefore, are more resistant to extinction.

It is also expected that narrowly adapted taxa are more vulnerable to environmental fluctuations and are, therefore, at higher risk of extinction (Vrba, 1984, 1989; Owen-Smith, 1987; Stanley, 1991; Turner and Paterson, 1991). In addition, specialized taxa are also under stronger directional selection pressures and thus they are expected to be more prone to speciate than lineages of generalists (Vrba, 1984, 1989). In contrast, generalist species are expected to have greater extinction resistance even during periods of mass extinction (Stanley, 1990; Smith and Jeffrey, 1998). In this analysis, I use the range of food items in the diet of carnivoran species as an indicator of their degree of trophic specialization.

Although it has been suggested that aspects of social structure may have affected the evolutionary history of mammal taxa (Berta, 1987; Vrba, 1989; Gittleman and Purvis, 1998), no empirical study has addressed this topic. Here, I explore whether differences in sociality level are associated with differences in speciation and/or extinction rates across carnivoran lineages. Mathematical models indicate that highly social carnivoran lineages in which reproduction and/or survival of individuals depends upon cooperation among group members may be more vulnerable to extinction (Courchamp *et al.*, 1999a,b, 2000; Purvis *et al.*, 2000).

The carnivoran groups included in this study (Caninae, Ursinae, Felinae and Hyaenidae) were selected because they display a wide range of morphological variation and diversity of social and ecological interactions. Moreover, information is available on the fossil record, biology and ecology of extant species in these groups, as well as phylogenetic information that supports their monophyletic status.

METHODS

Independent variables

Data on body size, diet and social organization were extracted from the published literature. Categories for dependent variables were defined as follows:

Body size

Because reported average body sizes in the literature are based on different sample sizes, weighted average body size was estimated for each species. Values for males and females and values reported for populations in different geographical regions were combined in the estimation of weighted average body sizes. Body size was analysed both as a continuous and as a discrete character. In the first case, species values were multiplied by 10 first and then logarithmically transformed. Multiplying by 10 is required because species weighing less than 1 kg will yield negative values after logarithmic transformation and this, in turn, will affect the estimation of body size contrasts. In the second case, three body size categories were defined using percentiles based on the weighted average body size of 213 carnivore species. The resulting body size categories are: small, carnivoran species whose average body weight is < 2.4 kg; medium, species with average body weight > 2.4 and < 8.8 kg; and large, species that have an average weight > 8.8 kg.

Diet

Species were designated as carnivores, insectivores or herbivores if vertebrates, insects or plant material constitute at least 60% of their diet, respectively. Carnivore species in which vertebrates make up more than 60% of the diet and that usually take prey larger than themselves were categorized as hypercarnivorous. Species in which no food type makes up to 60% of the diet were designated omnivorous.

Sociality level

Three main categories for sociality level were used. Species categorized as ‘highly social’ live in social groups that occupy and defend a territory, maintain a social hierarchy, and often hunt, feed and den together. The ‘highly social’ category includes species that live in packs, prides and clans. In canids, in particular, groups of highly social species include both adult females and males as non-reproductive helpers and there is a pattern of strict reproductive suppression. The family-living category includes species in which groups are formed by individuals that den together, spend the entire year together and may forage cooperatively. Usually, the offspring of these mated pairs disperse before the next litter, but some – especially females – may remain with the mated pair until or after the birth of the next litter. Solitary species are those in which individuals have an established home range with no cohabiting mate or pack; the only long-lasting relationship is between females and their offspring.

I combined two or more character states into new categories and then tested for their association with differences in speciation and extinction rates. For instance, it is expected that narrowly adapted taxa (i.e. strict carnivorous/insectivorous/herbivorous) have significantly higher extinction and speciation rates than generalist lineages. To test this hypothesis, I grouped together herbivorous, insectivorous and flesh-eater lineages in a single category of 'specialists' and compared their mean speciation and extinction rates against that of lineages in which no particular food category makes up to 60% of the diet.

Speciation and extinction rates

Speciation and extinction rates were estimated based on the diversity of extant and extinct species. Speciation rate (S) was estimated in two different ways:

$$S_1 = N_s/t \tag{1}$$

$$S_2 = (N_s \times 100)/(N \times t) \tag{2}$$

where N_s is the number of recorded extinct and extant species in a clade and t is the estimated time since diversification of a given clade in millions of years and corresponds to the absolute age of the oldest known fossil record within a clade. The time of clade origination 't' was corrected using the 'ghost lineage' concept (Norell, 1992). Thus, if the oldest known fossil record of a given clade was younger than the corresponding record for its sister group, the time of origination of the former clade was extended to match that of its sister. Equation (1) normalizes* for time, allowing comparisons of clades with different recorded durations. Equation (2) normalizes for both time and total number of species (N) originated across all clades being compared. Equation (2) is the percent of species originated within a lineage per million years relative to the total number of carnivore species originated across all carnivore groups being analysed. Extinction rate (E) was calculated as the percentage of taxa per million years that became extinct (N_e) within a given clade as follows:

$$E = (N_e \times 100)/(N_s \times t) \tag{3}$$

The recorded number of species within a clade may be influenced by the effect of taphonomic biases. Thus, to obtain a more accurate estimate of clade diversity, it is necessary to introduce a correction for factors affecting the chances of fossilization and recovery of fossil data. In an analysis of taphonomic biases affecting the fossil record of carnivoran taxa, Muñoz-Durán and Van Valkenburgh (in prep.) found that differences in habitat breadth do not affect the chances of fossilization or recovery of carnivoran fossils. However, they found that the diversity of small, medium and large carnivorans could be

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* I used 'normalize' in the sense of dividing by time of clade origination and/or total number of species. I did this to obtain a metric that allows the comparison of clades that differ in either or both of those factors.

underestimated by about 30%, 14% and 7%, respectively, due to the effect of taphonomic biases. Based on these findings, I applied a correction by multiplying the recorded number of extinct species by 1.42, 1.16 and 1.07 in clades of small, medium and large carnivorans, respectively. Taphonomic biases associated with differences in sampling effort are more difficult to control for and, in the present study, they are expected to have a greater effect on the records of Central and South American carnivoran lineages. These are geographical areas that require not only major efforts in palaeontological research, but also in the systematization of the existing data.

Taxonomic identifications of fossil specimens may also lead to an erroneous estimation of the true number of fossil species belonging to a given clade. Because of this, I assembled a conservative list of extinct species by removing synonymies and *nomina dubia*.

Analysis of phylogenetic patterns

Phylogenetic trees

The canid phylogeny (Fig. 1) is that proposed by Muñoz-Durán (submitted) based on the combined analysis of morphological and mtDNA data. I followed Tedford *et al.* (work in progress) regarding the phylogenetic relationships of the extinct canid genera Leptocyon, Eucyon, Theriodictis, Protocyon and Dusicyon. I used the ursid phylogeny of Talbot and Shields (1996) (Fig. 2) but excluded the giant panda lineage, which is consistently located at the base of the modern ursid radiation (Nash and O'Brien, 1987; Talbot and Shields, 1996). The reason for this is the uncertainty about the time of radiation of the Ursavini group (including the genera *Indarctos*, *Agriotherium* and *Ursavus*). It is unclear whether the

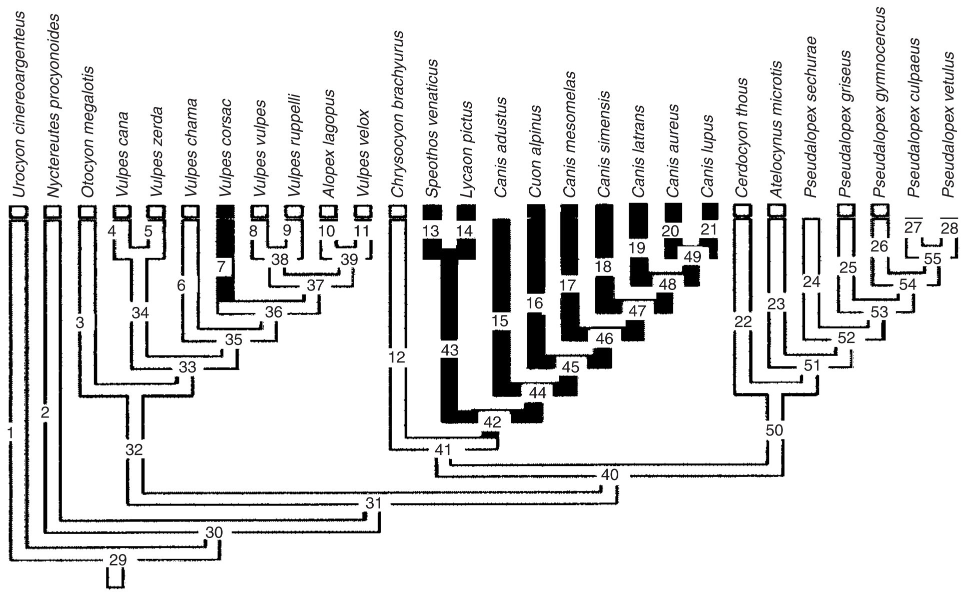

Fig. 1. Distribution of character states for sociality in the Caninae. Phylogeny of the Caninae based on the combined analysis of morphological and mtDNA data (Muñoz-Durán, submitted).

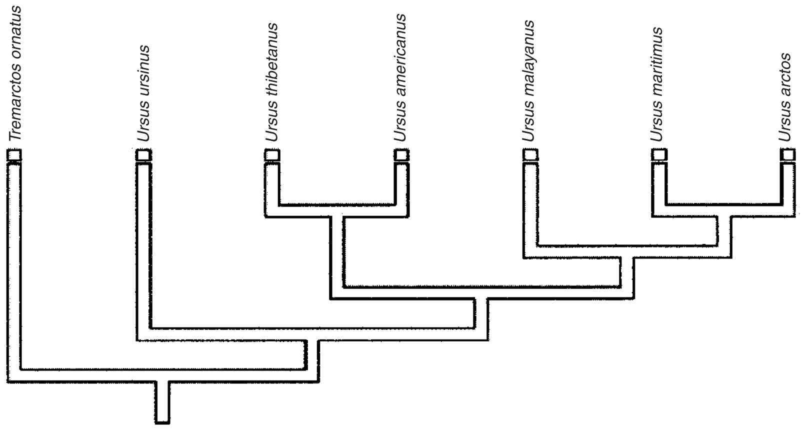

Fig. 2. Distribution of character states for sociality in the Ursinae. The phylogeny of the Ursinae is that of Talbot and Shields (1996). The lineage of the panda (*Ailuropoda melanoleuca*) is excluded.

Ursavini radiate before or after the divergence of the giant panda (*Ailuropoda melanoleuca*) lineage. Thus, by excluding the giant panda lineage, I was certain about the monophyletic condition of the remaining Ursini–Tremarctini group. I also used Jenks and Werdelin's (1998) hyaenid phylogeny derived from molecular data (Fig. 3). Although this phylogenetic arrangement differs from that obtained from morphological and palaeontological data (Werdelin and Solounias, 1991, 1996; Werdelin *et al.*, 1994), the molecular phylogeny data provide stronger evidence for the relationships among the extant hyenas (Jenks and Werdelin, 1998). I followed Werdelin and Solounias (1996) regarding the phylogenetic relationships of fossil hyaenid genera. The phylogenetic tree for the Felinae (Fig. 4) is that of Mattern and McLennan (2000), which is based on a total evidence analysis of 12SrRNS, 16S rRNA, NADH-5, cytochrome b sequences, and karyological and morphological characters.

Reconstructing ancestral behaviours

Ancestral character states for diet and sociality were estimated using a standardized method based on outgroup comparisons and parsimony algorithms as implemented in MacClade 3.07 (Maddison and Maddison, 1992). I code these traits as unordered. When equivocal ancestral character states were produced, both ACCTRAN (accelerated transformations) and DELTRAN (delayed transformations) reconstructions were tried. Body size was analysed both as a discrete and as a continuous character. In the former case, ancestral character states were estimated as explained above and body size was coded as an ordered character. In the second case, ancestral character states were estimated using 'squared-change parsimony' (Rogers, 1984; Huey and Bennett, 1987).

Correlated evolution of organismal and group level traits

Once ancestral character states were reconstructed, I tested the null hypothesis of independent character evolution using the 'concentrated-changes test' (Maddison, 1990). The concentrated-changes test is designed to determine whether an observed number of gains and losses in a dependent, binary character is significantly associated with the distribution

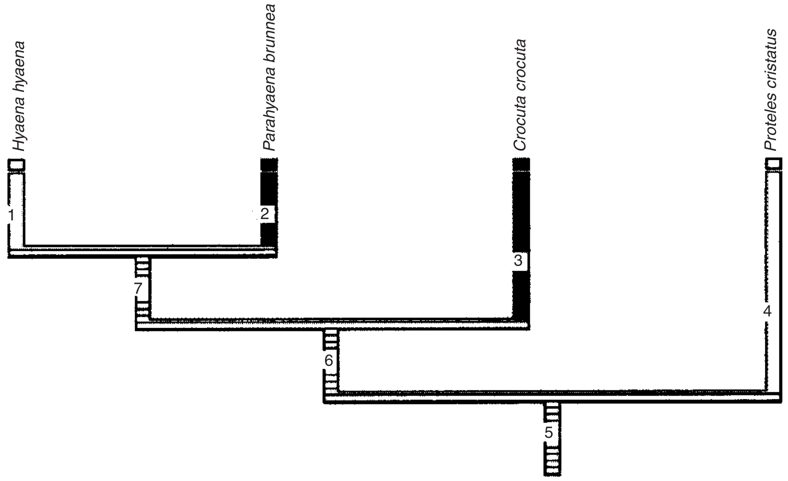

Fig. 3. Distribution of character states for sociality in the Hyaenidae. The phylogeny of the extant Hyaenidae is derived from molecular data (Jenks and Werdelin, 1998).

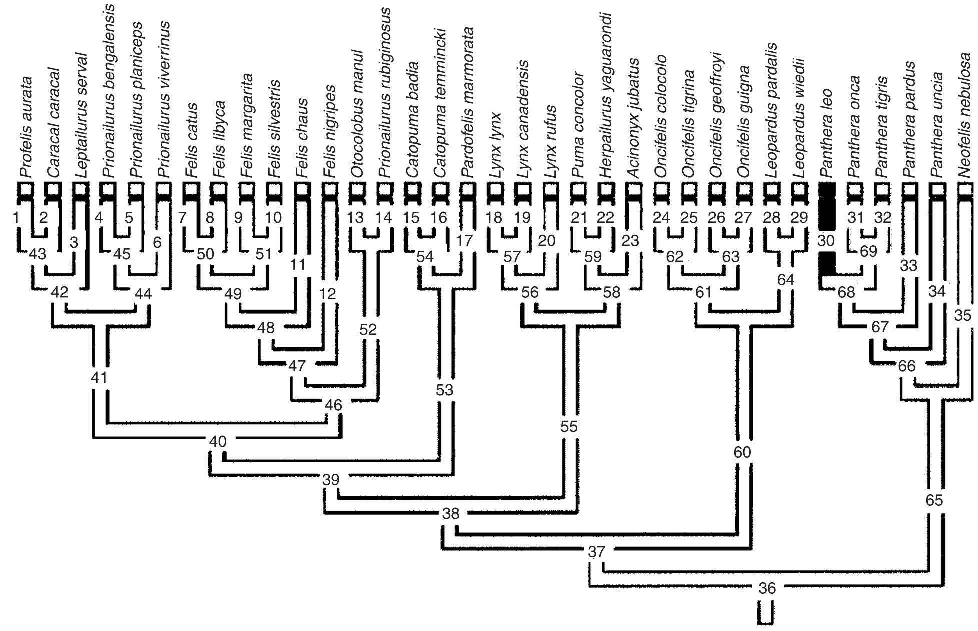

Fig. 4. Distribution of character states for sociality in the Felinae. The phylogeny of the Felinae is based on a total evidence analysis (Mattern and McLennan, 2000).

of character states of another binary character along a phylogeny (Maddison, 1990; Harvey and Pagel, 1991; Maddison and Maddison, 1992; Werdelin and Tullberg, 1995). The concentrated-changes test explicitly treats one of the variables as the independent or causal variable and the other as the dependent variable. It then searches for evidence that the likelihood of the dependent variable changing is higher in the presence of one category of the independent variable than in the presence of the other. The concentrated-changes test uses the null hypothesis that a trait is uniformly distributed on a phylogeny. Thus, a significant concentration test value indicates that a given state of the independent variable may enable gains in the dependent variable (Maddison and Maddison, 1992).

Clade comparisons

In the case of discrete variables, clades with contrasting ancestral character states were selected to test for differences in their speciation and extinction rates. In most cases, lineages sharing similar ancestral character states due to common ancestry were excluded from the set of comparisons. These taxa must not be treated as independent data points, since doing so will violate the assumption of phylogenetic independence. This will also lead to an overestimation of the number of degrees of freedom, which, in turn, will have a misleading effect on other statistics, particularly *P*-values. However, the above cannot be treated as a rigid rule. In some instances, taxa that do share a given ancestral character state because of common ancestry may be considered as independent observations for statistical analyses depending on the specific details of their evolutionary history. These details include the length of time since clades diverged and specific events of dispersal and colonization of novel environments. Another precaution I followed to avoid overcounting was that, once a clade was selected as a data point for the analysis, no other younger clade within the former was also included. This was done because ancestral and derived clades sharing the same character state do not represent independent data points. Once clades for comparison were identified, Wilcoxon-Mann-Whitney and Kruskal-Wallis (*k*-sample) tests were used to assess if differences in discrete character states were associated with differences in speciation and extinction rates among lineages. Since the direction of association between differences in body size, diet and sociality level with evolutionary rates had previously been hypothesized, one-tailed probabilities were reported.

The effect of differences in body size, studied as a continuous variable, was analysed in a similar way to the MacroCAIC approach (Agapow and Isaac, 2002). Contrasts of body size and evolutionary rates were calculated for higher nodes (genus and other more inclusive clades). Associations between contrast in body size and contrast in evolutionary rates were assessed through Pearson correlation.

RESULTS

Data on body size, diet and sociality level for extant species are presented in Table 1. Information on diversity of extant and extinct taxa, including first known times of taxa origination, is provided in Appendix 1. Clades for comparisons were selected after ancestral character states were calculated (Figs 1–4). These clades are presented in Table 2, together with the approximate time of clade origination (t), the time of clade origination corrected using the 'ghost lineage' approach (t'), the number of extinct species in a clade (N_e), the number of extinct species corrected for taphonomic biases (N_eTB), the number of extant species (N_1) and the total number of species in a clade (N_sTB). Speciation (S_1 and S_2) and extinction (E) rates of clades are also shown in Table 2. Contrasts of body size and speciation and extinction rates are shown in Table 3.

The results of the concentrated-change test indicate that body size, diet and sociality have evolved independently from each other in the carnivoran groups analysed. Although few correlations were found between some characters states of independent variables, these

Table 1. Body size, diet and sociality of extant carnivoran species

Group	Genera	Species	Common name	Body size (kg)	Body size*	Diet*	Sociality*
Canids	*Urocyon*	*U. cinereoargenteus*	Grey fox	4	M	O	F-S
	Nyctereutes	*N. procyonoides*	Racoon-dog	4.73	M	O	F
	Otocyon	*O. megalotis*	Bat-eared fox	4.07	M	I	F
	Vulpes	*V. cana*	Blanford's fox	0.89	S	I	F
		V. zerda	Fennec fox	1.33	S	O	F
		V. chama	Cape fox	2.65	S	O	F
		V. corsac	Corsac fox	2.09	S	C	HS
		V. vulpes	Red fox	4.8	M	O	F
		V. ruppelli	Ruppell's sand fox	1.62	S	I	F
		V. velox	Swift fox	2.35	S	O	F
	Alopex	*A. lagopus*	Arctic fox	3.8	M	C	F
	Chrysocyon	*C. brachyurus*	Maned wolf	22.94	L	O	F-S
	Speothos	*S. venaticus*	Bush dog	7.9	M	HC	HS
	Lycaon	*L. pictus*	African wild dog	22.75	L	HC	HS
	Cuon	*C. alpinus*	Dhole	17.5	L	HC	HS
	Canis	*C. adustus*	Side-striped jackal	8.85	L	O	?
		C. mesomelas	Black-backed jackal	8.1	M	C	HS
		C. simensis	Simien jackal	14.5	L	C	HS
		C. latrans	Coyote	13.35	L	C	HS
		C. aureus	Golden jackal	6.21	M	C	HS
		C. lupus	Grey wolf	41.1	L	HC	HS
	Cerdocyon	*C. thous*	Crab-eating fox	5.61	M	O	HS
	Atelocynus	*A. microtis*	Small-eared dog	8.83	L	O	F-S
	Pseudalopex	*P. sechurae*	Sechuran fox	4.5	M	O	?
		P. griseus	Argentine grey fox	3.84	M	O	F
		P. gymnocercus	Pampas fox	4.4	M	O	F
		P. culpaeus	Culpeo fox	10.4	L	O	?
		P. vetulus	Hoary fox	3.8	M	O	?

Table 1.—*continued*

Group	Genera	Species	Common name	Body size (kg)	Body size*	Diet*	Sociality*
Ursids	*Tremarctos*	*T. ornatus*	Spectacled bear	110	L	O	S
	Ursus	*U. ursinus*	Sloth bear	101.5	L	I	S
		U. thibetanus	Asiatic black bear	103.54	L	O	S
		U. americanus	American black bear	105.5	L	H	S
		U. malayanus	Sun bear	45	L	O	S
		U. maritimus	Polar bear	365.5	L	C	S
		U. arctos	Brown bear	298.9	L	O	S
Hyaenids	*Proteles*	*P. cristatus*	Aardwolf	11	L	I	S
	Crocuta	*C. crocuta*	Spotted hyena	65.15	L	HC	HS
	Hyaena	*H. hyaena*	Striped hyena	26.5	L	O	S
	Parahyaena	*H. brunnea*	Brown hyena	39	L	C	HS
Felids	*Neofelis*	*N. nebulosa*	Clouded leopard	20	L	C	S
	Panthera	*P. uncia*	Snow leopard	37.5	L	C	S
		P. pardus	Leopard	40	L	C	S
		P. tigris	Tiger	136	L	C	S
		P. onca	Jaguar	56	L	C	S
		P. leo	Lion	135	L	HC	HS
	Leopardus	*L. wiedii*	Margay	4.3	M	C	S
		L. pardalis	Ocelot	11.8	L	C	S
	Oncifelis	*O. guigna*	Kodkod, guina, huina	2.2	S	C	S
		O. geoffroyi	Geoffroy's cat	4.5	M	C	S
		O. colocolo	Pampas cat	3.4	M	C	S
		O. tigrina	Tiger cat, oncilla	2.2	S	C	S

Acinonyx	*A. jubatus*	Cheetah	40.5	L	C	S
Herpailurus	*H. yaguarondi*	Jaguarundi	5.2	M	C	S
Puma	*P. concolor*	Puma	51.9	L	C	S
Lynx	*L. rufus*	Bobcat	10.5	L	C	S
	L. lynx	Eurasian lynx	19.9	L	C	S
	L. canadensis	Canadian lynx	9.8	L	C	S
Catopuma	*C. badia*	Bornean bay cat	2.4	S	C	S
	C. temmincki	Temminck's golden cat	10	L	C	S
Pardofelis	*P. marmorata*	Marbled cat	3.5	M	C	S
Prionailurus	*P. rubiginosus*	Rusti-spotted cat	1.5	S	C	S
Otocolobus	*O. manul*	Manul, Pallas's cat	3.0	M	C	S
Felis	*F. nigripes*	Black-footed cat	1.4	S	C	S
	F. chaus	Jungle cat	5.4	M	C	S
	F. silvestris	Wildcat	4.1	M	C	S
	F. margarita	Sand cat	2.5	S	C	S
	F. libyca	African wild cat	4.3	M	C	S
	F. catus	Domestic cat	3.9	M	C	S
Prionailurus	*P. viverrinus*	Fishing cat	6.8	M	C	S
	P. bengalensis	Leopard cat	2.4	S	C	S
	P. planiceps	Flat-headed cat	1.9	S	C	S
Leptailurus	*L. serval*	Serval	11.7	L	C	S
Caracal	*C. caracal*	Caracal	11.6	L	C	S
Profelis	*P. aurata*	African golden cat	7.6	M	C	S

* *Body size categories*: S, small; M, medium; L, large. *Categories for diet*: O, omnivorous; I, insectivorous; H, herbivorous; C, carnivorous; HC, hypercarnivorous. *Categories for sociality level*: S, solitary; F, family groups; F-S, family groups and solitary individuals; HS, highly social, including packs, prides, clans, etc.

Table 2. Clades used for comparative analyses

Group	Phylogenetic hypothesis	Clade	t	t'	N_e	N_eTB	N	N_s	N_sTB	S_1	S_2	E	Body size (S/M/L)	Body size (S-M/L)	Body size (S/M-L)	Diet (OM/E)	Diet (C/O)	Sociality (S/F/HS)	Sociality (S-F/HS)	Sociality (S/F-HS)
Canids	MPR	32	9	9	11	15	13	24	28	3.11	1.30	5.95		S-M			O	F	S-F	
		52	2.5	3.3	9	10	5	14	15	4.55	1.89	20.20		S-M*						
		50	4.4	7.8	12	14	7	19	21	2.69	1.12	8.55	M	S-M*		OM	O	F	S-F	
		41	4.7	7.8	45	49	11	56	60	7.69	3.21	10.47	L	L						
		33	9	9	9	13	12	21	25	2.78	1.16	5.78	S		S					
		40	7.8	9.7	57	63	18	75	81	8.35	3.48	8.02			M-L					
		45	4.6	7.8	41	45	7	48	52	6.67	2.78	11.09				E				
		42	4.6	7.8	44	48	10	54	58	7.44	3.10	10.61					C	HS	HS	
		Root	9.7	34	80	92	34	114	126	3.71	1.54	2.15								F-HS
	ACCTRAN	32	9	9	11	15	13	24	28	3.11	1.30	5.95				E				
		50	4.4	7.8	12	14	7	19	21	2.69	1.12	8.55				OM				
		42	4.6	7.8	44	48	10	54	58	7.44	3.10	10.61				E				
Ursids – Panda		Root	9.4	29	27	29	7	34	36	1.24	0.52	2.78	L	L	M-L		O	S	S-F	S
Felids		46	11.6	11.6	4	5	8	12	13	1.12	0.47	3.32	M	S-M						
		61	2.5	9.4	1	1	4	5	5	0.53	0.22	2.13	M	S-M						
		65	3.7	11.6	2	2	6	8	8	0.69	0.29	2.16	L	L						
		55	7.3	7.3	7	8	7	14	15	2.05	0.86	7.31	L	L						
		Root	11.6	20	18	20	37	55	57	2.85	1.19	1.75			M-L	E	C	S	S-F	S
Hyaenids	MPR	1	3.5	3.7	1	1	1	2	2	0.54	0.23	13.51				OM	O	S	S-F	S
		2	3.7	3.7	1	1	1	2	2	0.54	0.23	13.51				E	C	HS	HS	F-HS
		3	3.7	9	13	14	1	14	15	1.67	0.69	10.37				E	C	HS	HS	F-HS
		4	2	9	1	1	1	2	2	0.22	0.09	5.56				E	O	S	S-F	S
		Root	3.7	9	16	17	4	20	21	2.33	0.97	8.99	L	L	M-L					
	ACCTRAN	6	3.7	9	15	16	3	18	19	2.11	0.88	9.36					C	HS	HS	F-HS
		4	2	9	1	1	1	2	2	0.22	0.09	5.56					O	S	S-F	S

Note: t, approximate time of clade origination (millions of years); t', the time of clade origination corrected using the ‘ghost lineage’ approach; N_e, number of extinct species in clade; N_eTB, number of extinct species corrected for taphonomic biases; N, number of extant species; N_sTB, total number of species in a clade; S_1 and S_2, speciation rates; E, extinction rate; MPR, most parsimonious reconstruction. *Body size categories*: S, small; M, medium; L, large. *Diet categories*: OM, omnivorous; E, specialist; C, carnivorous; O, others. *Categories for sociality*: S, solitary; F, family; HS, highly social. Entries distinguished with an asterisk (*) indicate clades that can be used for a specific analysis.

Table 3. Contrasts of body size and speciation (S_1 and S_2) and extinction (E) rates

Group	Clades	Body size contrasts	S_1 contrasts	S_2 contrasts	E contrasts
Canids	23-52	0.232	−3.939	−1.832	−19.481
	51-22	0.077	2.727	1.163	−3.409
	16-46	0.197	−4.231	−2.326	−1.416
	14-13	0.477	0.000	−0.465	−50.000
	43-44	0.081	−4.744	−2.683	−6.410
	12-42	0.266	−5.000	−2.922	−3.896
	41-50	0.294	5.256	2.027	2.062
	40-32	0.318	6.667	2.481	2.778
	3-33	0.246	−0.778	−0.930	2.116
	31-2	0.027	9.889	4.548	−2.083
	30-1	0.069	9.900	4.512	−0.124
Ursids	1-9	0.026	0.426	−0.099	2.881
Hyaenids	2-1	0.168	0.270	0.000	0.000
	3-7	0.233	1.333	0.517	4.762
	6-4	0.5	1.889	0.827	3.704
Felids	2-1	0.183	0.500	0.116	12.500
	3-43	0.111	0.000	−0.233	−8.333
	42-44	0.249	1.000	0.116	6.250
	41-46	0.281	0.259	−0.200	−1.642
	54-17	0.136	3.000	0.930	33.333
	40-53	0.003	1.552	0.601	0.113
	21-22	1.001	0.541	0.126	13.514
	23-59	0.356	0.870	0.202	10.145
	58-56	0.238	0.822	0.127	3.995
	55-39	0.365	0.690	−0.361	2.061
	64-61	0.272	0.426	0.000	2.128
	38-60	0.163	2.931	1.083	0.443
	66-35	0.224	3.182	1.268	12.987
	65-37	0.368	−0.690	−1.564	−0.780

Note: Differences in body size among carnivoran lineages are not associated with differences in their speciation and extinction rates ($r_{S1} = -0.153$, $P = 0.215$; $r_{S2} = -0.166$, $P = 0.195$; and $r_E = -0.012$, $P = 0.475$; $n = 29$).

correlations were not consistent across all clades. For instance, most gains of hypercarnivorous diets are concentrated in lineages of large canids ($P = 0.019$) and large felids ($P = 0.042$). However, this association cannot be extended to the ursid and hyaenid clades, which are composed exclusively of large species that have great variation in dietary habits. Similarly, hypercarnivory is significantly associated with group living in canids ($P = 0.019$), but this association does not hold true for the felid and hyaenid clades. In the former, hypercarnivory is characteristic of large, solitary species in the *Panthera*, *Puma* and *Lynx* genera. In the latter, the large and highly social brown hyena (*Parahyaena brunnea*) has a diet that, although based on vertebrate flesh, cannot be classified as hypercarnivorous because of their marked dietary flexibility.

The results of the comparative analyses indicate that, during the recent history of canid, ursid, felid and hyaenid evolution, lineages of highly social carnivorans have had significantly higher extinction rates than lineages of solitary or family-living carnivorans. Although this result is only significant at the 0.05 level, it is consistent across all different reconstructions tried (MPR: Mann-Whitney $Z = -1.69$, $P = 0.046$, $N = 9$; ACCTRAN for Hyaenids: Mann-Whitney $Z = -1.94$, $P = 0.027$, $N = 7$). Differences in sociality level do not appear to be associated with differences in speciation rates of carnivoran lineages. In addition, no significant associations were found among differences in speciation or extinction rates across carnivoran lineages with differences in body size and diet. Because no significant and consistent correlations were found between independent variables, the effect of sociality on extinction rates is free of constraints imposed by body size or diet.

DISCUSSION

The findings of this research must be interpreted with caution. Two factors may affect the calculation of evolutionary rates in the present study: missing species and incompleteness of stratigraphic ranges. To account for the first of these limitations, I introduced a control for taphonomic biases related to body size that improves the estimation of diversity of extinct species within clades. Tackling the second issue is more complicated. Although quantitative methods to correct for the incompleteness of the fossil record have been proposed (Strauss and Sadler, 1989; Springer, 1990; Marshall, 1991, 1997; Solow, 1996), it was not possible to estimate confidence intervals for the stratigraphic ranges of carnivorans. This is because available methods not only require information on first and last recorded appearances, but also on all occurrences of the taxa between the first and last known records. Such data are difficult to collect for groups in the present study because they have broad geographical distributions. The limitations relate to the lack of relevant rock outcrops in some areas, to low sampling effort for some taxa and geographical regions, and to the access to existing data that have not been published in international journals, among others.

The equations used to estimate speciation and extinction rates assume that these are continuous processes during the geological history of a clade and that evolution proceeds in a gradual fashion. Although processes of taxa origination and extinction occur constantly, discrete events of exceptionally high extinction and speciation rates are common (Raup and Sepkoski, 1982; Vrba, 1985; Jablonski, 1986; Lewin, 1986; Raup, 1986). Thus, dividing by time of clade origination in the above equations may, under some circumstances, misrepresent the real dynamics of speciation and extinction within clades. However, the speciation and extinction equations I used in this analysis are not expected to misrepresent the evolutionary dynamic of the clades analysed. This is because the time interval covered in this study is restricted to the last few million years of carnivoran evolution, from the Miocene to the Present. Events of generalized high speciation or extinction during that time were of relatively low intensity (Raup, 1991; Jablonski, 1994; Alroy, 1996), and probably affected in a similar fashion all carnivore groups included in the analysis. Furthermore, dividing by time of clade origination in the above equations was intended to provide a summary of the evolutionary dynamic of a clade during a relatively short period of geological time. In this regard, the speciation and extinction equations I used must be understood as indices of rates rather than rates proper. In addition, estimates of speciation and extinction rates normalized by time in this study are strictly necessary, since the clades compared have different times of origination.

The speciation and extinction equations in this analysis also assume that clade diversity is steady during a clade geological history (Rosenzweig, 1995). Rosenzweig and Vetault (1992) proposed speciation and extinction metrics that avoid the above assumption. Their equations are based on the Malthusian equation for population growth and take into account the fact that speciation and extinction repeatedly take place during the evolution of a clade. Unfortunately, Rosenzweig and Vetault's (1992) equations cannot be calculated for clades represented by only one extant species. This is the case for all four clades of hyenas included in the present analysis. Therefore, the use of Rosenzweig and Vetault's equations would have led to even smaller sample sizes for comparison of clades in the present study. I calculated speciation and extinction rates using Rosenzweig and Vetault's (1992) equations for 17 clades included in this analysis that have more than one extant species (Table 4). When I compared the new results with the ones obtained with the equations I used in the present study, I found similar rankings of speciation (Spearman rank correlation $r = 0.77$, $P \ll 0.001$) and extinction rates (Spearman rank correlation $r = 0.946$, $P \ll 0.001$). Consequently, it is expected that similar patterns of speciation and extinction will be obtained when applying evolutionary metrics that do not assume constant diversity of clades.

Compared with cross-taxon and sister taxa comparison approaches to analyse correlates of evolution, the approach I have used leads to a smaller sample size and, therefore, to a higher chance of type II errors – the retention of a false null hypothesis. This may be the

Table 4. Comparison of speciation and extinction rates calculated using equations that assume steady clade diversity (like the ones used in this paper: S_1, S_2 and E respectively) and equations that do not make such an assumption (Rosenzweig and Vetault's, 1992, speciation rate, σ, and extinction rate, μ)

Group	Clade	S_1	S_2	σ	E	μ
Canids	32	3.1111	1.2963	0.6412	0.0595	0.3562
	52	4.5455	1.8939	1.7070	0.2020	1.2193
	50	2.6923	1.1218	0.8316	0.0855	0.5821
	41	7.6923	3.2051	1.8138	0.1047	1.5064
	33	2.7778	1.1574	0.6024	0.0578	0.3263
	40	8.3505	3.4794	1.4022	0.0802	1.1043
	45	6.6667	2.7778	2.1205	0.1109	1.8711
	42	7.4359	3.0983	1.8696	0.1061	1.5744
	Root	3.7059	1.5441	0.3929	0.0215	0.2891
Ursids	Root	1.2414	0.5172	0.3914	0.0278	0.3243
Felids	46	1.1207	0.4670	0.3073	0.0332	0.1280
	61	0.5319	0.2216	0.1966	0.0213	0.0492
	65	0.6897	0.2874	0.2162	0.0216	0.0618
	55	2.0548	0.8562	0.6220	0.0731	0.3554
	Root	2.8500	1.1875	0.2808	0.0175	0.1003
Hyaenids	Root	2.3333	0.9722	1.0269	0.0899	0.8729
	6	2.1111	0.8796	1.0986	0.0936	0.9765

Note: The two types of equations lead to similar rankings of speciation and extinction rates as indicated by Spearman rank correlation: $r_{S1\sigma} = 0.77$, $P \ll 0.001$; $r_{S2\sigma} = 0.77$, $P \ll 0.001$; and $r_{E\mu} = 0.946$, $P \ll 0.001$.

reason why the pattern of association between sociality level and extinction rates observed in this study was scarcely significant at the 0.05 level. However, the above limitation is compensated, to some extent, by the use of all known information about the evolutionary history of a group of taxa. The approach outlined in this paper also avoids using excessive or unjustified assumptions about evolutionary processes, about origination and extinction dynamics, about molecular clocks and other conjectures associated with other methodological approaches.

Phylogenetic patterns

Body size

The lack of a significant association between differences in body size and speciation and extinction rates in carnivorans is in line with previous research across several mammal clades (Vrba, 1989; Gittleman and Purvis, 1998). Gittleman and Purvis' (1998) analysis of the association between differences in body size and species richness in the Carnivora and Primates shows that there is a weak and inconsistent tendency for lineages of small-bodied caniforms to have a higher species richness. However, this tendency was not present in the feliform and primate lineages. Their interpretation of this result is that, although mammal body size is relevant on an ecological scale, perhaps it does not play a major role on a macroevolutionary scale. In a recent study, Purvis *et al.* (2000) also found that differences in body size of extant carnivorans are not associated with differences in extinction risk.

Trophic specialization

Differences in trophic specialization (diet) are not associated with differences in speciation or extinction rates across the carnivoran lineages studied. The results do not agree with the prediction that specialized taxa are more vulnerable to extinction than taxa with more generalized habits (Vrba, 1984, 1989; Owen-Smith, 1987; Stanley, 1991; Turner and Paterson, 1991). One explanation for this departure may be that, in times of prey scarcity or large-scale environmental changes, hypercarnivorous species may shift to prey on the most abundant vertebrate species in their habitat. Alternatively, hypercarnivorous species can temporarily turn to a more opportunistic and omnivorous diet, expanding the range of food items that they could use in their habitats. The above alternatives are available for animal groups that display some ecological or behavioural plasticity. It is not the case, for example, of sea urchins, in which the theoretical prediction of the relationship between trophic specialization and extinction risk has been confirmed (Smith and Jeffrey, 1998). Smith and Jeffrey's (1998) analysis of extinction selectivity among sea urchins at the end of the Cretaceous shows that sea urchins with specialized feeding habits were affected more by a decrease in phytoplankton abundance and other marine environmental changes than urchin species with more generalized and omnivorous feeding habits.

The lack of an association between differences in trophic specialization and speciation rates in carnivores also contrasts with Vrba's (1984, 1989) findings in a study of African ungulates. Vrba's results indicate that pure grazer and browser clades have higher speciation rates than clades that combine both grazing and browsing. The discrepancy between the pattern in carnivorans and ungulates may result from a higher susceptibility of herbivorous organisms to environmental changes, resulting in stronger directional selection pressures and, therefore, in higher speciation and/or extinction rates (Vrba, 1984, 1989; Owen-Smith, 1987; Raup and Boyajian, 1988; Raup, 1992; Lessa and Farina, 1996).

Sociality

Although the observed pattern is scarcely significant at the 0.05 level, sociality is the only variable studied that is related to extinction proneness of carnivoran lineages. The association between social organization and rates of evolution has not been explored in previous analyses of macroevolutionary patterns in mammals. The only related work that I am aware of is Purvis and colleagues' (2000) comparative analysis of extinction risk of extant carnivoran and primate species. In that study, Purvis *et al.* utilized group size as a proxy of social organization to analyse correlates of extinction risk. Their results indicate that group size is not significantly associated with extinction risk on extant carnivores. The contrast between Purvis and co-workers' results and those reported here can be explained in terms of the 'effect of the present'. Over-hunting, habitat fragmentation, habitat loss, introductions of species and other human-related causes have affected most populations of extant carnivorans regardless of their social organization. Under these circumstances, other factors such as small geographical range, trophic levels, population density and slow life histories may become better predictors of species vulnerability to extinction than social structure (Purvis *et al.*, 2000).

Explaining the pattern

Sociality in carnivorans may have evolved as a strategy to prey upon large, gregarious ungulates (Martin, 1989), and to gain advantages in the context of intra-guild competition. This, in turn, places social carnivores in an ecological setting in which the intensity of competition is extreme, and in an ecological and evolutionary pathway in which the risk of extinction is high. The pattern found in this study can be explained by the combined effect of the following factors:

Intense competition or Van Valkenburgh's 'dog-eat-dog' world

The evidence for intense interspecific competition among large, hypercarnivorous and highly social carnivorans is overwhelming (for reviews, see Palomares and Caro, 1999; Van Valkenburgh, 2001). The data on competitive interaction among extant carnivorans show that there is a hierarchy of dominance within the carnivoran guild that is arranged along body and group size, with large social species at the top of this hierarchy (Eaton, 1979; Palomares and Caro, 1999; Van Valkenburgh, 2001). The advantages of group living are supported by the observation that small social carnivores tend to win disputed kills over solitary or smaller groups of larger bodied species. Social carnivores are not only able to displace but also kill other carnivores that weigh up to 12 times their own body mass (Palomares and Caro, 1999). This pattern of carnivoran intra-guild competition is common across a wide range of habitats worldwide (Palomares and Caro, 1999; Van Valkenburgh, 2001). Thus, it is possible that a similar pattern arose from the competitive interaction among ancestral populations of the modern carnivorans (Van Valkenburgh, 2001). The data also show that competition among large, hypercarnivorous, social species is fierce and results not only in a variety of strategies to find, pursue, bring down and defend prey from competitors, but also in interspecific killing, competitive exclusion, reduction of population densities and even local extinction of the more vulnerable species. Even if competition by itself does not lead to extinction, it can keep populations of certain carnivores at low levels. Under these circumstances, the Allee effect and the lower effective population sizes of social carnivorans make them more vulnerable to extinction than solitary species.

Social carnivores, extinction risk and the Allee effect

The combination of intense competition and the consequences of the Allee effect may help to explain the significantly higher extinction rates observed in the lineages of highly social carnivores. The Allee effect refers to the positive relationship between population density and growth rate at low population densities; it is usually referred to as 'inverse density dependence' (Courchamp *et al.*, 1999a,b). Hence, once competition has pushed a carnivoran population to low densities, the rate of growth of that population is reduced. At low population density, the population becomes more susceptible to the effect of inbreeding, genetic drift, outbreaks of disease, reductions in prey availability, skewed sex ratios and other processes of genetic, demographic and environmental stochasticity (Pimm *et al.*, 1988; Lande, 1993; Bennett and Owens, 1997; Courchamp *et al.*, 1999a,b, 2000). The combined effect of stochastic process and sustained competitive pressure may drive the population to even lower densities. The Allee effect predicts that, once a population reaches a given low density threshold, the population growth rate becomes negative and the risk of extinction becomes even greater (Courchamp *et al.*, 1999a).

Compared with solitary species, the consequences of the Allee effect are more severe in social species in which reproduction and survival depend on cooperation (Courchamp *et al.*, 1999a,b, 2000; Stephens and Sutherland, 1999). Courchamp *et al.* (2000), using mathematical models, showed that enemies (predators, parasites or competitors) decrease the group size of cooperators (obligately cooperative breeding species) more than that of non-cooperators, thereby increasing the relative risk of extinction of cooperator groups. They also demonstrated that the Allee effect operating at the social group level can also lead to low population densities and, therefore, to increased risks of population extinction. Courchamp *et al.* (1999b, 2000) suggested that the high rates of group and population extinction observed in African wild dogs result from an Allee effect related to the existence of a critical number of helpers below which groups cannot subsist.

The combined effect of strong intra-guild competition and the Allee effect may lead to the extinction of highly social carnivoran species in which: (1) reproduction and/or offspring survival depends on alloparental care; (2) successful hunting of large prey relies on the coordinated action of group members; and (3) successful defence of carcasses and territories is positively associated with group size.

Reproductive suppression and reduced effective population sizes

Reproductive suppression is common in social carnivorans in which reproduction and/or offspring survival depends upon a group rather than on individual organisms. Thus, in populations of these species, the number of breeding entities is proportional to the number of social groups, not to the number of adult males and females (Stephens and Sutherland, 1999). Therefore, social carnivoran species with reproductive suppression (i.e. wolf-like canids) have lower effective population sizes compared not only with solitary carnivorans, but also with other lineages of social carnivorans that do not show reproductive suppression (i.e. lions and hyenas). As mentioned before, the Allee effect predicts higher vulnerability to extinction of social species in general. Because of the reduction in effective population size brought about by reproductive suppression, species that display this strategy must enter the phase of negative population growth at relatively higher population densities than species without reproductive suppression. The reason for this is that, at similarly low population densities, carnivoran species with lower effective population sizes must be more susceptible to stochastic processes than species with higher effective population sizes (Vucetich *et al.*, 1997). The above may explain why the lineage of the wolf-like canids, in which reproductive suppression is common (Moehlman and Hofer, 1996), has one of the highest extinction rates among all carnivore lineages.

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APPENDIX 1

List of extant and extinct species in included lineages and corresponding first known times of origination (FKTO, millions of years). The list of cited references is given in Appendix 2

Genera	Species	FKTO	References
Canids			
Leptocyon +		34	13, 151, 157
	L. sp. *A*	34	157
	L. mollis	30	157
	L. douglassi	30	157
	L. vulpinus	24.3	13, 107, 151
	L. delicatus	28	157
	L. vafer	16.3	13, 100, 103, 104, 151
	L. gregorii	23.5	13, 151
	L. sp. *B*	17	157
	L. leidyi	18.8	157
	L. tejonensis	12	157
Metalopex +	*M. macconnelli*	10	157
	M. merriami	9	157
	M. bakeri	7.5	157
Urocyon	*U. progressus* +	7.5	13, 151, 157
	U. webbi +	7.5	157
	U. galushai +	5	157
	U. citrinus +	2	157
	U. minicephalus +	1.2	157
	U. cinereoargenteus	2.4	13, 62, 151
	U. littoralis	0.01	
Nyctereutes	*N. donnezani* +	4.0	7, 16, 21, 27, 43, 49, 58, 64, 71, 75, 132, 133, 157
	N. megamastoides +	3.5	16, 27, 43, 75, 127, 133, 157
	N. abdeslami +	2.5	19
	N. tingi +	4.4	75
	N. terblanchei +	1.9	26, 115, 116, 119, 123
	N. sinensis +	4.5	17, 27, 35, 75, 157
	N. vinetorum +	0.05	121
	N. procyonoides	0.5	91, 157

Otocyon	*O. recki* +	2.5	3, 26
	O. curvipalatus +	2	157
	O. megalotis	1	3, 26
Vulpes	*V. stenognathus* +	9	3, 13, 27, 101, 151, 157
	V. kernensis +	9	157
	V. praecorsac +	3.2	3, 157
	V. alopecoides +	3.2	16, 43, 133
	V. pattisoni +	1.9	3, 26
	V. praeglacialis +	1.5	43, 129, 130, 157
	V. beihaiensis +	3.3	72
	V. chikushanensis +	0.5	157
	V. galacticus +	3.5	132
	V pulcher +	1.9	3, 26
	V. bengalensis	?	
	V. cana	?	
	V. chama	1	3, 26, 117, 118
	V. corsac	0.8	56
	V. ferrilata	?	
	V. ruppelli	?	
	V. pallida	?	
	V. velox	4	151
	V. macrotis	2	100
	V. vulpes	5	3, 26, 43, 55, 56, 82, 86, 134
	V. zerda	1.9	3, 26
Alopex	*A. lagopus*	1.8	134
Chrysocyon	*C. arcticus* +	4.4	13, 157
	C. brachyurus	1.5	40, 104
Speothos	*S. pacivorus* +	0.1	100, 104, 107, 157
	S. venaticus	0.1	104, 157
Xenocyon +	*X. lycaonoides*	1.5	157
	X. dubius	2.3	157
	X. stehlini	0.4	157
Lycaon	*L. pictus*	1.0	3, 26, 113, 119, 1122, 123, 157
Cuon	*C. majori* +	2.6	13
	C. javanicus +	0.7	94, 157
	C. priscus +	2.6	13, 36, 43
	C. alpinus	0.8	13, 36, 43, 53, 82, 86
Eucyon +	*E. davisi*	7.8	13, 77, 104, 151
	E. zhoui	4	77, 157
	E. monticinensis	7	7, 43, 77
	E. minor	2.6	77
	E. odessana	4	77
Canis	*C. ferox* +	6	42, 151, 157
	C. lupoides +	6	157
	C. lepophagus +	4.8	13, 35, 104, 120, 135, 151
	C. euthos +	2.5	157
	C. feneus +	0.5	157

Appendix 1—*continued*

Genera	Species	FKTO	References
	C. antonii +	2.3	3, 8, 10, 27, 130, 157
	C. chihliensis +	2.3	157
	C. edwardii +	3	1, 35, 62, 101, 151
	C. etruscus +	1.5	3, 43, 120, 127, 129, 130, 157
	C. michauxi +	4	3, 7, 16, 43, 49
	C. adoxus +	4.1	7, 16, 43, 49
	C. mosbachensis +	1	10, 58, 157
	C. variabilis +	1	157
	C. palmidens +	2.3	157
	C. falconeri +	1.5	8, 10, 40, 58, 120, 127, 129, 130, 157
	C. arnensis +	2.6	10, 58, 120, 127
	C. cautleyi +	1	3, 157
	C. africanus +	1.9	8, 26, 130
	C. brevirostris +	1.9	26
	C. atrox +	1.9	26
	C. priscolatrans +	0.6	100, 103, 50, 104, 120, 157
	C. armbrusteri +	1.5	62, 101, 103, 104, 151, 157
	C. dirus +	0.1	3, 40, 100, 101, 103, 104, 107, 151, 157
	C. cedazoensis +	2.8	1, 2, 151, 157
	C. gezi +	1	40, 44, 100, 104, 107, 157
	C. nehringi +	0.3	40, 100, 104, 107
	C. texanus +	1.2	40, 103, 151
	C. ameghinoi +	0.3	100
	C. senezensis +	2.6	49
	C. palustris +	2	103
	C. spelaeus +	2	103
	C. vitastensis +	0.73	126
	C. adustus	3.2	26, 119, 123, 131
	C. aureus	2.5	19, 26, 131
	C. mesomelas	3.5	26, 114, 116, 117, 118, 119, 122, 124, 131
	C. latrans	1.5	3, 101, 50, 65, 120, 157
	C. lupus	2.6	10, 35, 43, 55, 56, 82, 86, 127
	C. rufus	0.1	151, 157
	C. simensis	?	
Cerdocyon	*C. avius* +	4.4	13
	C. ensenadensis +	1.5	27, 100, 104, 107
	C. lydekkeri +	0.3	107
	C. thous	0.3	157
Atelocynus	*A. microtis*	0.01	41
Protocyon +	*P. scagliarum*	3.3	40, 44, 100, 104, 107
	P. orcesi	0.3	40, 100, 104, 107
	P. troglodytes	1.5	40, 100, 104, 107
Theriodictis +	*T. platensis*	2.5	40, 44, 100, 104, 107
	T. tarijensis	1.5	40, 100, 104, 107
Dusicyon +	*D. australis*	0.3	40, 41, 104
	D. avus	0.3	40, 41, 100, 104, 107

Pseudalopex	*P. proplatensis* +	2.5	44, 100, 107
	P. peruanus +	0.3	41, 104, 107
	P. culpaeus	0.7	44, 104, 107
	P. griseus	1.5	100, 107
	P. gymnocercus	2.5	44, 100, 104, 107
	P. sechurae	0.3	104, 107
	P. vetulus	0.3	104
Ursids			
Plionarctos +		9.4	11, 101, 151
	P. edensis	7	3, 11
	P. telonensis	1.5	67
	P. stehlini	1.5	67
Tremarctos	*T. floridanus* +	3.3	2, 11, 101, 50, 104, 151
	T. ornatus	2.5	11
Arctodus +	*A. pristinus*	3	2, 6, 11, 62, 101, 103, 104, 151
	A. simus	2.1	2, 6, 11, 100, 101, 103, 50, 104
	A. angustidens	1.9	2, 6, 11, 107
	A. bonariensis	1.9	38
	A. pamparus	2.5	38, 44, 107
	A. brasiliensis	1.9	38
	A. enectum	1.9	38
	A. candiottii	1.5	107
	A. debilis	1.5	107
	A. tarijense	0.3	107
	A. vetustus	?	107
Ursus	*U. minimus* +	5.5	11, 34, 43, 127, 128
	U. abstrusus +	4.9	2, 101, 151
	U. etruscus +	4.3	34, 43, 127, 128, 129
	U. savini +	1.5	34
	U. deningeri +	1.8	3, 34, 43, 57, 127
	U. boeckhi +	5	128
	U. spelaeus +	0.7	34, 35, 39, 43, 55, 57, 82, 83, 84
	U. praearctos +	0.7	43
	U. schertzi +	1.8	67
	U. mediterraneus +	1.8	67
	U. wenzensis +	3.5	21
	U. yinanensis +	2.6	93
	U. ursinus	?	
	U. thibetanus	2.5	34, 54, 67, 84, 91
	U. americanus	3	2, 50, 34, 104, 151
	U. malayanus	?	
	U. maritimus	0.35	2, 34,
	U. arctos	2.5	2, 26, 34, 39, 43, 55, 57, 84, 128
Hyaenids			
Proteles		2	64, 114, 117, 118, 119, 122, 123
	P. amplidentus +	?	
	P. cristatus	1.5	100, 123
Pachycrocuta +	*P. perrieri*	5	16, 27, 19, 43, 56, 58, 127
	P. pyrenaica	4.8	16, 28, 43
	P. brevirostris	3.2	27, 43, 58, 85, 116, 119, 122, 124, 127, 129

Appendix 1—*continued*

Genera	Species	FKTO	References
	P. simensis	1.8	98
	P. bellax	1.8	26, 115
Adrocuta +	*A. eximia*	9	10, 16, 17, 43, 58, 59, 64, 78
Crocuta		3.7	80,149
	C. dietrichi +	3.5	47
	C. 'ultra' +	2.5	19
	C. sivalensis +	?	
	C. spelaea +	1.8	43, 55, 103
	C. honanensis +	1.8	98
	C. n. sp. *A* +	Plio.	148
	C. n. sp. *B* +	Pleist.	148
	C. crocuta	3.7	26, 43, 58, 114, 115, 116, 117, 118, 119, 122, 123, 124, 125, 127, 149
Hyaena	*H. hyaena*	3.5	26, 64, 66, 78, 111, 119, 123, 125, 149
	H. makapani +	3.3	148, 149
Parahyaena	*Parahyaena* n. sp. +	3.7	148, 149
	P. brunnea	3	26, 66, 114, 115, 116, 117, 118, 119, 122, 123, 124, 149
Felids			
Neofelis	*N. nebulosa*	?	
Panthera	*P. schaubi* +	2.2	16, 43, 85
	P. gombaszoegensis +	1.8	9, 43, 85, 127, 155
	P. pardus	3.7	19, 26, 55, 85, 114, 115, 116, 117, 118, 119, 122, 123, 124, 156
	P. leo	3.7	26, 82, 85, 101, 114, 115, 116, 117, 119, 122, 123, 156
	P.onca	2.4	2, 44, 101, 104, 107
	P. uncia	1.4	
	P. tigris	1.8	92, 85, 103, 156
Pardofelis	*P. marmorata*	?	
Lynx	*L. longignathuss* +	7.3	12, 151
	L. issiodorensis +	5.3	16, 26, 32, 2, 43, 105, 127
	L. rufus	4.4	32, 2, 62, 69, 101, 50, 104, 105
	L. pardinus	0.5	81, 82, 105
	L. lynx	0.1	26, 81, 105
	L. canadensis	0.3	2, 69, 105
Herpailurus	*H. yaguarondi*	1.9	2, 69, 106
Caracal	*C. brevirostris* +	4	105
	C. caracal	4	26, 105, 114, 115, 116, 117, 119, 122
Leptailurus	*L. serval*	3.2	26, 114, 117, 119, 119
Prionailurus	*P. viverrinus*	?	
	P. rubiginosus	?	

	P. bengalensis	0.2	154
	P. planiceps	?	
Profelis	*P. aurata*	?	
Catopuma	*C. teilhardii* +	1	105
	C. badia	?	
	C. temmincki	2.6	105
Acinonyx	*A. studeri* +	4.6	2, 37, 62, 100, 151
	A. pardinensis +	3.8	9, 16, 43, 100, 103, 58, 68, 85, 127
	A. aicha +	2.5	19
	A.trumani +	0.85	2
	A. jubatus	3.5	26, 114, 115, 116, 117, 118, 119, 122, 123
Puma	*P. lacustris* +	3.7	2, 50, 69, 101, 105, 151, 156
	P. concolor	2.15	12, 2, 37, 50, 100, 101, 68, 104
Otocolobus	*O. manul*	?	
Felis	*F. christoli* +	6.3	43
	F. attica +	11.6	9, 25, 58, 71
	F. wenzensis +	3.5	21
	F. antediluviana +	11.6	71
	F. silvestris	3.8	43, 55, 19
	F. bieti	?	
	F. chaus	?	
	F. margarita	?	
	F. nigripes	?	
	F. libyca	1.8	26, 114, 117
Leopardus	*L. rexroadensis* +	9.4	12, 69, 101, 103, 104, 151, 156
	L. amnicola +	0	151
	L. wiedii	3	30, 2, 69, 156
	L. pardalis	0.3	2, 33, 69, 101, 104, 107
	L. jacobitus	?	
Oncifelis	*O. vorohuensis* +	2.5	104
	O. guigna	?	
	O. geoffroyi	0.05	44
	O. colocolo	?	
	O. tigrina	?	

Note: + = extinct taxa.

APPENDIX 2

List of references cited in Appendix 1. To avoid making the paper extremely long by in including the complete references, this list is intended as a guide to the information sources of the data presented in Appendix 1. Upon request, the author will provide the complete list of references

Reference	Authors	Reference	Authors
1	Nowak (1979)	47	Werdelin and Lewis (2000)
2	Kurtén and Anderson (1980)	48	Wang (1994)
3	Savage and Russell (1983)	49	Rook *et al.* (1991)
4	Benton (1993)	50	Cassiliano, M.L. (1999)
5	Erdbrink, D.P.B. (1993)	51	Lewis and Berger (1998)
6	Mones, A. (1985)	52	Werdelin *et al.* (1994)
7	Rook, L. (1992)	53	Baryshnikov, G. (1996)
8	Rook, L. (1994)	54	Crégut-Bonnoure, E. (1996)
9	Anton and Turner (1997)	55	Dimitrijevic, V. (1996)
10	Rook, L. and Torre, D. (1996)	56	Holec, P. (1996)
11	Hunt, R.M. (1998)	57	Tsoukala, E. (1996)
12	Martin, L.D. (1998)	58	Werdelin and Turner (1996)
13	Munthe, K. (1998)	59	Werdelin and Solounias (1990)
14	Natural History Museum, Turkey	60	Werdelin (1988a)
15	O'Brien, S.J. (1996)	61	Werdelin (1988b)
16	Mein, P. (1989)	62	Berta (1995)
17	Qiu, Z. (1989)	63	Berta (1998)
18	Alpagut *et al.* (1989)	64	Bernor, R.L. *et al.* (1996)
19	Geraads, D. (1997)	65	Lucas *et al.* (1997)
20	Ginsburg, L. (1989)	66	Werdelin and Barthelme (1997)
21	Kowalski, K. (1989)	67	Fistani (1993)
22	Barry and Flynn (1989)	68	Van Valkenburgh *et al.* (1990)
23	Savage, R.J.G. (1989)	69	Werdelin, L. (1985)
24	Hunt and Solounias (1991)	70	Berta (1981)
25	Solounias, N. (1981)	71	Werdelin, L. (1996)
26	Savage, R.J.G. (1978)	72	Qiu and Tedford (1990)
27	Mills and Hofer (1998)	73	Zhanxiang Qiu and Guoqin Qi (1990)
28	Rieger, I. (1981)	74	Zong and Jiang (1991)
29	Mills, M.G.L. (1982)	75	Tedford and Zhanxiang (1991)
30	Oliveira, T.G. (1998a)	76	Zhanxiang *et al.* (1991)
31	Oliveira, T.G. (1998b)	77	Tedford and Zhanxiang (1996)
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33	Murray and Gardner (1997)	79	Kurtén and Werdelin (1988)
34	Kurtén, B. (1976)	80	Lewis and Werdelin (1997)
35	Olsen, S.J. (1985)	81	Kurtén and Granqvist (1987)
36	Erdbrink, D.P.B. (1991)	82	García and Arsuaga (1998)
37	Morgan and Seymour (1997)	83	Grandal-D'Anglade and Vidal (1997)
38	Trajano and Ferrarezzi (1994)	84	Crégut-Bonnoure, E. (1997)
39	Hanni *et al.* (1994)	85	Turner and Antón (1996)
40	Berta, A. (1988)	86	Cardoso (1996)
41	Berta, A. (1987)	87	De Bonis and Koufos (1991)
42	Miller and Carranza-Castañeda (1998)	88	Tang *et al.* (1995)
43	Alberdi *et al.* (1997)	89	Tedford, R. (1995)
44	Tonni *et al.* (1992)	90	Tong, Y. (1995)
45	Bonfiglio and Insacco (1992)	91	Tong *et al.* (1995)
46	Morales *et al.* (1998)	92	Xie *et al.* (1994)

93	Li (1993)
94	Ma and Tang (1992)
95	Huang (1993)
96	Qi (1989)
97	Qiu and Qi (1989)
98	Huang (1989)
99	Zong (1987)
100	UC Museum of Paleontology[1]
101	FMNH[2]
102	TNHC[3]
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104	Van Valkenburgh, B. (1991)
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127	Gliozzi *et al.* (1997)
128	Rustiony and Mazza (1993)
129	Palmqvist and Gibert (1992)
130	Palmqvist *et al.* (1999)
131	Van Valkenburgh and Wayne (1994)
132	Ginsburg, L. (1998)
133	Koufos, G.D. (1993)
134	Wayne *et al.* (1987b)
135	Kurtén, B. (1986)
136	Youngman, P. (1994)
137	Youngman, P. (1993)
138	Anderson, E. (1994)
139	Graham and Graham (1994)
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141	Bryant, H.N.
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147	Goldman, D. *et al.* (1989)
148	Werdelin, L. (2001) personal communication
149	Werdelin and Turner (1996)
150	MSW – Smithsonian Institution
151	Alroy, J. (2000)[5]
152	Wilson (1999)
153	Slattery *et al.* (1994)
154	Masuda *et al.* (1996)
155	Janczewski *et al.* (1995)
156	Johnson *et al.* (1996)
157	Tedford, R. (2001) personal communication

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[2] Florida Museum of Natural History, web page: http://www.flmnh.ufl.edu/scripts/DBs/VP_UF_pub.asp

[3] Texas Natural History Collection of the Texas Memorial Museum of the University of Texas at Austin.

[4] Peabody Museum of Natural History, Yale University, web page: http://www.peabody.yale.edu/collections/vp/

[5] Alroy (2000) North American fossil mammal systematics database: http://www.nceas.ucsb.edu/~alroy/nam/search.html.