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Why 'carnivore conservation'?

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At present carnivore biologists are at an especially tough crossroads. Species are going extinct at a rate 100 times the natural background rates. With only around 5% of the planet's land surface protected in some form, continued habitat loss will produce much greater extinction rates, with potential disappearance of up to half of the world's species (May *et al.*, 1995; Pimm *et al.*, 1995). Critical conservation decisions are needed, at split-second timing, about which species to save, the best way to protect them, and how to divide resources for protecting and managing some taxa over others; indeed, the science of conservation biology is often characterized as the 'crisis discipline' (Soulé, 1985). Our intuition is to protect what we know and like. This is difficult with carnivores given that no one has a neutral position with them – they are loved or hated. On the one hand, carnivores are viewed as beautiful, powerful, and majestic; carnivores *are* 'megacharismatic'! It is unsurprising that visitors to the London Zoo recently indicated (Carvell *et al.*, 1998) that five out of their top 10 most popular animals are carnivores (Sumatran tiger, Persian leopard, Asiatic lion, meerkat, otter). On the other hand, carnivores are seen as the personification of evil, as exemplified in Theodore Roosevelt's description of the wolf as 'the beast of waste and desolation'. Such extremes in our perception of carnivores will continually work in favor and against conserving them.

The pressing issue is how to give carnivores priority, financially and intellectually, over other taxa when undertaking conservation measures. Carnivores *are* very expensive, not to mention labor intensive – radio collars, helicopters, laboratory costs all add up to millions of either dollars or pounds to carry out any successful conservation project on even a single species. Are carnivores this special? Relative to the disproportionate costs for doing conservation on them, can we rationalize that carnivores are worth it?

CARNIVORES ARE SPECIAL, OR ARE THEY?

In terms of species diversity, carnivores are not that unusual. From 4629 species (among 1135 genera) in the class Mammalia (Wilson & Reeder, 1993), the 271 species in the order Carnivora rank as the fourth largest group behind the Rodentia (2021), Chiroptera (925), and Insectivora (428). Size is not everything, though. The relevant question is: What do carnivores represent in terms of biodiversity, both historically and at present? Another picture emerges, one that gets at the question of whether carnivores are a special case for saving, even at high costs.

Evaluating what to preserve for the future necessarily involves understanding the past. The geological record shows that carnivores have often faired relatively well compared to other taxa. In contrast to many other mammals, carnivores have not gone through dramatic fluctuations in species numbers. General patterns of extinction versus origination rates in genera of Pleistocene carnivores suggest relatively high rates of new species appearances (Simpson, 1953; Gingerich, 1984). More detailed study of the fossil record over the past 44 million years in North America shows that carnivore species have remained relatively stable, despite a decline in herbivore diversity after the middle Miocene (Van Valkenburgh & Janis, 1993). That is, carnivores do not reveal directional evolutionary patterns, but rather are characterized by repeated evolution of certain ecomorphs such as cat-like and bone-cracking species (Martin, 1989). For example, sabertooth-like species have evolved independently at least three times (Felidae, Nimravidae, Creodonta), hyena-like species at least twice (Canidae, Oxyaenidae), and large dog-like predators at least four times (Canidae, Amphicyonidae, Ursidae, Hyaenidae). Such trends are consistent with predictions for extinction rates (McKinney, 1998) – of all mammalian orders, 24% of all Carnivora species are 'threatened' and, based on branching (birth–death) models measuring the number of species extinctions per unit time (McKinney, 1998), show the third lowest projected extinction rate (behind bats and rodents). Further, if we calculate the mean extinction rate of carnivores relative to the initial number of species in the group, the projected duration of the order is 2486 years, a fairly healthy duration relative to the median of 1179 years across mammals as a whole. So, despite the attention carnivores have received, extinction rates are not especially dire for the group as a whole. The causal reasons for this 'resilience' are obviously important to understand in conservation biology and emphasize the need to learn more about why some carnivores evade extinction (see Weaver *et al.*, 1996). However, an extremely important qualifier is needed here – even though carnivores may fair relatively *well as a whole*, historical and current patterns of extinction clearly indicate that large, carnivorous species with restricted ranges are highly threatened. Unless prompt measures are taken, carnivores may be represented largely by raccoons, coyotes, red foxes, and common weasels.

Extinction vulnerability among species is frequently expressed by particular biological traits (e.g., Terborgh, 1974; Wilson, 1987; Gittleman, 1994; McKinney, 1997; Purvis *et al*., 2000b). These include: the number of species in a monophyletic group; species with narrow geographical ranges; species with only one or a few populations, small population sizes, or declining population sizes; species with low population densities; species requiring large home ranges; species with large body sizes; species with little genetic variability; species with specialized niche requirements; and species that are harvested or hunted by people. In many ways, these are exactly the characteristics that reflect the biology of carnivores!

Undoubtedly, the underlying reason for carnivores withstanding such multiple extinction risks is their tremendous variability, both within and across species. The observed range for an array of important biological traits is greater for carnivores than any other mammalian order (see Eisenberg, 1981; Gittleman, 1989, 1996; Macdonald, 1992), including:

- Body sizes range from the 100 g least weasel to the gigantic 800 kg or so polar bear.
- Reproductive rates are as low as one offspring every seven years, as in some black bears, to as high as three litters per year with eight young in a litter, as in some populations of mongooses.
- Carnivores are found in virtually every habitat or vegetational zone, from short grassland (meerkat) to sparse woodland (dwarf mongoose) to desert (fennec fox) to thick tropical forest (kinkajou) to oceanic waters (sea otter).
- Home ranges may be fairly small (0.55 km^2: coatis; 0.20 km^2: red foxes) to extremely large and non-defensible (1500–2000 km^2: wild dogs), with worldwide geographical ranges lying between the restrictive island forms (e.g., island gray fox or Cozumel coatimundi) to the massive distribution of nearly 70 million km^2 of the red fox.
- Social structure ranges from spatially solitary individuals, with only brief encounters during breeding (ermine) to those species that form monogamous pair bonds (golden jackal) to those that live in extended social groups with as many as 80 individuals (spotted hyena).

Of course, overlaid onto this interspecific variation is considerable variation and flexibility within species. For example, in gray wolves adults weigh from 30 to 80 kg, litter size varies from one to 11, and populations are found in every vegetational habitat except tropical forests and arid deserts.

Within such variability lies our answer to the question of whether carnivores are special – a resounding 'yes', especially when we think about variation in carnivores explicitly in the context of conservation. This point is more compelling if we think in terms of species lists and classification schemes. Species are often classified into the following categories: indicator species, those that reflect critical environmental damage; keystone species, those that play a pivotal role in ecosystems; umbrella species, those that require large areas and thus, if protected, will protect other species; flagship species, those popular species that attract much attention; and, vulnerable species, those species most likely to become extinct. Each classification informs whether a species or taxonomic group are pivotal in terms of conservation status and the relative attention they receive for protection and management. It is quite remarkable that not only do many single carnivore species fit *all of these labels* but that there are entire carnivore clades that match these criteria. In the end, we suggest that an important reason why carnivore conservation should receive resources and attention, even perhaps disproportionately so, is that carnivores are renaissance taxa, involving a synthesis of conservation problems, causal factors and solutions.

SUCCESSES AND PROBLEMS – WORKING TOGETHER IN CARNIVORE CONSERVATION

Many classic examples of successful conservation biology involve carnivores. Problems of genetics, reintroduction, management, animal behavior and behavioral ecology, ecology, and policy all use carnivores as basic test cases in the literature. This is not surprising. Motivation for using carnivores obviously relates to their megacharismatic status, though equally important is their intrinsic variability. If we can sort out complex carnivores, we are bound to solve problems of other taxa. Importantly, we need to recognize a unique feature of our successes – collaboration. Take two examples. First, synthetic studies in ecology, population biology, behavioral ecology, and wildlife management have been critical for showing significant responses of carnivores to losses in prey (see Berger, 1998). Even experimental approaches to how prey respond to different kinds of olfactory and auditory stimuli in predators are informative for restoration of predator–prey communities. Secondly, the previously antagonistic relationship between field biologists and molecular geneticists is now coalescing into powerful conservation science. Studies on canids, felids, single species analyses of cheetah, black-footed ferrets, and tigers, all involve scientists in different disciplines showing that population fragmentation, genetic uniformity, and habitat loss are interrelated to such a degree that adopting only one approach is bound to miss important elements (Wayne, 1996).

These successes in more academically-related fields reveal an important contribution that we as carnivore conservationists need to acknowledge – conservation organizations studying other taxa are using carnivore-based studies. For instance, fundamental conservation goals are constructed from IUCN/SSC Action Plans on mustelids and viverrids (Schreiber *et al.*, 1989), otters (Foster-Turley *et al.*, 1990), procyonids and ailurids (Glatston, 1994), canids (Ginsberg & Macdonald, 1990), felids (Nowell & Jackson, 1996), African wild dog (Woodroffe *et al.*, 1997a), and Ethiopian wolf (Sillero-Zubiri & Macdonald, 1997). Occasionally, single-species conservation goals of carnivores are achieved so well that they leave a unique influence – in Nepal's Chitwan National Park, the population density of tigers is the highest in the world because of an unusually forceful blend of protection in the park, anti-poaching policies, and monitoring by governmental and non-governmental organizations (Dinerstein *et al.*, 1999). In turn, this has had a lasting effect on restoring ecological processes in the park, community-based ecotourism, and significant increases in the population density of other species (e.g., one-horned rhinoceroses). Newsletters formed from canid and small carnivore specialist groups are tremendous sources of information for conservation and management. These all are substantial contributions of which we as carnivore conservationists should be proud and continue to develop in conservation biology at large.

These successes should not disguise biases that have crept into conservation programs for carnivores. Two problems are particularly vexing. First, considerable attention in carnivore conservation has been focused almost exclusively on large carnivores. Indeed, large carnivores are often the textbook examples for prioritizing which species to save in conservation biology. As examples, large carnivores galvanize public opinion toward the greater goal of habitat conservation and the cessation of wildlife trade; the protection of large carnivores requires enormous reserves which protect other species; large carnivores occupy the top trophic levels of most food chains and offer stability to food webs; and large carnivores often are easy to breed in zoos and are notable successes in reintroduction programs. In sum, large carnivores reflect many critical problems of and solutions to carnivore conservation in general. The dilemma is to what extent is it effective to use large carnivores as a model and whether we should rethink this approach? For example, population decline and extinction are more likely with large species such as giant pandas and Siberian tigers. Conservation of large carnivores also affect negatively the conservation of other equally endangered species – cage space is expensive in zoos and conservation monies are limited. Despite large carnivores being used as symbols of conservation, they remain difficult to study and even detailed investigations of them often provide little return to basic science or consequential issues in conservation biology. For some large species there seem to be as many researchers working on them as there are individuals left in the wild. Should we redirect efforts toward other smaller and more abundant species, whose future is more certain and whose study provide potentially more significant lessons? In essence, we have made large carnivore species our symbols, bred them in zoos, displayed them to the public as synonymous with conservation. What do we do if our best efforts fail?

The other serious problem is what might be referred to as the 'human–carnivore interface'. Many examples could be given for this problem but generally the issue is that carnivore conservation becomes human-based, anthropocentric. For example, there is now whole-scale control of coyotes and foxes in the US and of cheetahs and jackals in Namibia. Should we be controlling carnivores in such situations, or should we adopt a strict ecological view, advocating complete uncritical protection? We need to work toward more balanced and flexible guidelines that allow control when it is effective and does not endanger populations.

These are only two problems that emphasize modern difficulties of carnivore conservation. There are many others that are just as pressing. The point is that we begin to assess what these problems are, what methods have worked and failed, and begin to focus on preserving carnivore species into the future.

PRIORITIZING PRESENT AND FUTURE PROBLEMS

Rare, elusive, dangerous – carnivores are difficult to study. This means collaboration is essential for successful conservation science. As problems become more severe, and they will, we must increase levels of collaboration to bring about quicker and more effective work. This was a primary motivation for organizing a Meeting, held 20 and 21 November, 1998 at The Zoological Society of London, in which we assembled for the first time a group of distinguished international researchers solely devoted to *carnivore conservation*, the result of which is the proceedings published herein. While acknowledging that not everything can be covered in this volume, the overarching goal was to assess where we are so to better carry out future studies of carnivore conservation. Within the framework of specific problems, we asked participants to organize chapters with reference to some broad issues:

- Are the methods and approaches effective in answering the question(s) at hand and to what extent are these carnivore-specific?
- How can we better assess which carnivore populations and species are more vulnerable?
- Might carnivore conservation be better served by prioritizing geographical areas or ecological communities rather than species-by-species (taxonomic) approaches?
- How can the science of carnivore conservation develop more effective means of communicating with the public and general environmental organizations, particularly when addressing human–carnivore conflicts?

In essence, the contributions in this volume lay out what we have accomplished thus far. More importantly, we hope that the papers here will help decide in which direction we head for carnivore conservation. As George Schaller (1996: p. 9) put it, 'We cannot ease the burdens of the past, but we can atone by assuring the carnivores of the future'.

PART I
Problems

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Past and future carnivore extinctions: a phylogenetic perspective

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INTRODUCTION

In many ways carnivores are an enigma for conservation biology. Consider the following. (1) The history of carnivores shows periods of devastating extinction rates, with 352 genera going extinct relative to the 129 currently living (McKenna & Bell, 1997; for comparison, primates and artiodactyls have lower rates but rodents much higher). (2) Episodes of extinction often have been followed by taxonomic replacement, as evidenced by saber tooths replacing themselves at least four times (Van Valkenburgh, 1999). (3) Of 4761 living mammal species spanning 11 orders, five have significantly more threatened species than expected (artiodactyls, insectivores, primates, perrissodactyls, sirenians) but carnivores are not one of them nor does any carnivore family have an unusually high level of threatened species (Mace & Balmford, 2000). (4) Carnivores carry the dubious distinction of facing more types of threat (e.g., habitat loss, effects of introduced species, rarity) than any other mammalian order yet no single carnivore taxon is unusually threatened. (5) Many carnivore species are the ultimate symbols of conservation biology (tigers, black-footed ferrets, red wolves, giant pandas) despite the high costs and extreme difficulties of conserving a single population or species of carnivore. Amazingly, the price tag for saving a single carnivore species (e.g., red wolf) may be over 4.5 million US dollars (Wayne & Gittleman, 1995). (6) Carnivores, and especially large felids, generally come out top in animal popularity in television polls, animal magazines, and among zoo visitors (Balmford *et al.*, 1998; Carvell *et al.*, 1998; Serpell, 1991).

Carnivores thus represent extremes of problems in conservation biology. Within one lineage, some species such as the red fox or the raccoon have virtually no risk of extinction – indeed, many are now considered pests in our largest cities – while others such as the giant panda and black-footed ferret are rapidly heading toward inevitable extinctions. Such diversity between closely related taxa suggests that carnivores are an ideal taxon to study the patterns and processes of extinction. In the words of Jared Diamond (1984a: p. 824), 'We need to understand why extinctions did befall some beasts in some places at some times, but not other beasts in the same places nor similar beasts at other places or times'. In this chapter, we show how taxonomic comparisons can identify what factors produce these disparate species conditions. We begin by stepping back from contemporary problems of carnivore conservation to consider historical patterns of extinction, using both available fossil data and new phylogenetic approaches. We then use this information to identify those carnivore taxa that were influenced by past extinction events. This guides our analysis of those factors that are important to consider as we develop plans to conserve present-day carnivore species.

PAST AND PRESENT TRENDS IN CARNIVORE EVOLUTION

The landscape of today's carnivores is very different from that which existed millions of years ago. Imagine small hyaenas with narrow, sharp teeth, and elongate, slender limbs; a gigantic mustelid (*Aelurocyon*) the size of a leopard; and bears of small size, living in social groups, having a meat-eating diet. These are only a fraction of the carnivore diversity that is now missing. Gone completely are the precursors to present-day carnivores, the 'miacoids' (a paraphyletic group including the stem canoids and stem feloids; Flynn & Galiano, 1982), and the creodonts that had three to four times more taxa than all of the 'modern' Carnivora. In relative terms, we now only have 129 extant genera compared to 352 fossil genera (McKenna & Bell, 1997). What characteristics of fossil carnivores contributed to their extinction? Recently, a number of excellent reviews have revealed important details about carnivore evolution (Flynn, 1996; Hunt, 1996; Janis *et al.*, 1998; Van Valkenburgh, 1999; Van Valkenburgh & Janis, 1993; Werdelin, 1996). The following is a brief summary of this literature that reveals general patterns in the fossil record, hints about causal factors influencing past extinction, and potential hypotheses for future risks of carnivore extinction.

Comparisons between studies of fossil carnivores and studies of extant species should take into account the different methodologies used in each case. Two types of palaeobiological information are used in our discussion. One is descriptive, essentially general information about the size, diet and overall ecomorphology of fossil forms emerging during the history of carni-