CHAPTER 1

Dramatis personae: an introduction to the wild felids

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Pallas's cat © John Tobias

What is a felid?

For those in tune with the intricate sophistication of cat behaviour, it may seem dusty minimalism to reduce what is special about them to the shapes of the bones in their ears. Nonetheless, felids belong to the cat-branch of the order Carnivora, formally the suborder Feloidea (cat-like carnivores), and traditionally have been distinguished from the Canoidea (dog-like carnivores) by the structure of the auditory bulla. That said, there is a deeper point to be made about the uniformity of the 36 extant species of wild felid, despite the fact that they range in size over two orders of magnitude from the massive Siberian tiger, *Panthera tigris altaica* (200–325 kg) to the dainty black-footed cat, *Felis nigripes* (1–2 kg), of southern Africa and diminutive rusty-spotted cat, *Prionailurus rubiginosus* (~1 kg), of India and Sri Lanka. All belong to a single subfamily of extant forms, the Felinae, and although their behaviour may be writ large or small, it is remarkably similar across them—cats are very distinctly cats (Macdonald 1992). In palaeogeological terms, the Felinae radiated relatively recently and rapidly in the late Miocene ~13–14 million years ago, with extinct and extant genera of the family Felidae derived from a common ancestor ~27 million years ago (Werdelin *et al.*, Chapter 2, this volume).

Felids are at an extreme among carnivores precisely because of their unanimous adherence to eating flesh, generally of vertebrate prey. Perhaps because they all face the same tasks—capturing (generally by ambush), subduing, and consuming their prey, and because of their relatively recent evolution, the morphology of most felids is remarkably similar (Kitchener *et al.*, Chapter 3, this volume). Felids are expert stalkers and killers, with specialized claws for holding and handling struggling prey before delivering a killing bite. Limbs are relatively long, with five digits on

Figure 1.1 Protracted claw of an immobilized African lion showing protective sheath, sharp ventral surface, and pointed tip © Joanne Loveridge.

the fore and four digits on the hind feet. The highly curved, laterally compressed, protractile claws are protected in sheaths when at rest and extended when needed (Fig. 1.1). However, the cheetah's (*Acinonyx jubatus*) claws, though partially protractile, are exposed at rest and the points blunted through contact with the ground. In this species, the claws may act as 'running spikes' providing traction for rapid acceleration in pursuit of prey. Relative to other carnivores, felids have shortened faces and rounded heads with 28–30 teeth adapted for dispatching prey and cutting flesh. Cat skulls have a less keel-like sagittal crest than canids and hyaenids and have wide zygomatic arches to accommodate large jaw muscles (Smithers 1983).

Ultimately, as for other mammals (e.g. Crook 1970; Bradbury and Vehrencamp 1976; Kruuk 1978; Jarman and Jarman 1979; Macdonald 1983; Macdonald *et al.* 2004b), felid bodies, lifestyles, societies, and species assemblages are reflections of their ecology. This chapter will introduce felids in the context of their role as predators, often apex predators, and as constituents of carnivore guilds and assemblages within their respective regional environments. We briefly discuss their intra- and interspecific relationships with each other and other members of the carnivore guild and the anthropogenic and conservation threats they face. The *dramatis personae*, intended to introduce the species discussed throughout this book, takes the form of 36 species vignettes. Finally, we present an analysis of the past 60 years of felid research to identify trends and potential gaps in the field of conservation and biology of wild felids.

Biogeography of felids

The wild Felidae inhabit all continents apart from Australasia and Antarctica (see Table 1.1), and occur on numerous islands, large (Borneo) and small (Trinidad). They utilize habitats as diverse as boreal and tropical forests, savannahs, deserts, and steppe—but many, particularly the smaller tropical species, are forest specialists, and 32 species occur in closed forest and woodland habitats (Nowell and Jackson 1996). Twenty-one species, almost 60% of all living felids, occur on the Asian continent, 14 of which are endemic there. Tropical and temperate Asian regions have the greatest number of cat species (12, with 10 found only in this biome), and Europe and the cold continental regions of Asia have seven species (with four found only here). Hot–dry south-west Asia also has seven species, all shared with Africa, although in south-west Asia the lion *Panthera leo* and cheetah *Acinonyx jubatus* have only small relict populations, and the tiger *P. tigris*

Table 1.1 Biogeographic occurrences of felid species. Species shown in bold typeface are endemic to the region.

Old World	New World
Asia—Tropical–Temperate	***Neotropics (Central and South America)***
Sunda clouded leopard *Neofelis diardi*	**Pampas cat *Leopardus colocolo***
Clouded leopard *Neofelis nebulosa*	**Geoffroy's cat *Leopardus geoffroyi***
Tiger *Panthera tigris*	**Guiña *Leopardus guigna***
Borneo bay cat *Pardofelis badia*	**Andean cat *Leopardus jacobbta***
Marbled cat *Pardofelis marmorata*	**Oncilla *Leopardus tigrinus***
Asiatic golden cat *Pardofelis temminckii*	**Margay *Leopardus wiedii***
Leopard cat *Prionailurus bengalensis*	Ocelot *Leopardus pardalis*
Flat-headed cat *Prionailurus planiceps*	Jaguar *Panthera onca*
Rusty-spotted cat *Prionailurus rubiginosus*	Puma *Puma concolor*
Fishing cat *Prionailurus viverrinus*	Jaguarundi *Puma yagouaroundi*
Jungle cat *Felis chaus*	Bobcat *Lynx rufus*
Leopard *Panthera pardus*	
Asia—Eurasia	***Nearctic (North America)***
Pallas's cat *Otocolobus manul*	**Canada lynx *Lynx canadensis***
Lynx *Lynx lynx*	Bobcat *Lynx rufus*
Iberian lynx *Lynx pardinus*	Ocelot *Leopardus pardalis*
Snow leopard *Panthera uncia*	Puma *Puma concolor*
Leopard *Panthera pardus*	Jaguarundi *Puma yagouaroundi*
Jungle cat *Felis chaus*	Jaguar *Panthera onca*
Wildcat *Felis silvestris*	
Asia—south-west Asia	
Caracal *Caracal caracal*	
Cheetah *Acinonyx jubatus*	
Lion *Panthera leo*	
Leopard *Panthera pardus*	
Jungle cat *Felis chaus*	
Sand cat *Felis margarita*	
Wildcat *Felis silvestris*	
Africa	
Black-footed cat *Felis nigripes*	
African golden cat *Caracal aurata*	
Serval *Leptailurus serval*	
Caracal *Caracal caracal*	
Cheetah *Acinonyx jubatus*	
Lion *Panthera leo*	
Leopard *Panthera pardus*	
Jungle cat *Felis chaus*	
Sand cat *Felis margarita*	
Wildcat *Felis silvestris*	

became extinct there decades ago, while in Africa the jungle cat *Felis chaus* occurs only in the vicinity of Egypt's Nile River. Africa has just three endemic species out of a total of 10. The Old World has twice the number of species (24) as the New World (12), and unlike the Canidae, no felid species straddle the divide, although two genera (*Lynx* and *Panthera*), do occur in both realms, and the Old World cheetah is grouped with the New World *Puma* clade (Werdelin *et al.*, Chapter 2, this volume). In the New World, only one species, *L. canadensis*, is exclusive to the northern realm; most species occur in the neotropics, with four found only in South America. Three Neotropical species have marginal ranges north of Mexico, and the Nearctic bobcat *L. rufus* extends south into north-central Mexico.

A few species have very large ranges spanning several continents. Leopards (*Panthera pardus*) are found from the Russian Far East and parts of Eurasia through tropical Asia, the Middle East, and throughout sub-Saharan Africa. The wildcat (*Felis silvestris*) is widely distributed in Africa, Asia, and Europe (Macdonald *et al.*, Chapter 22, this volume). The puma (*Puma concolor*) ranges across both North and South America, although it was extirpated a century ago from most of eastern North America. In contrast, some felid species are highly specialized and confined to limited areas of habitat in just a few countries. The Andean cat (*Leopardus jacobita*) occurs only in association with rocky outcrops in the arid zones of the high Andes, typically above 4200 m, a specialist predator of chinchillids (*Lagidium* spp.; Marino *et al.*, Chapter 28, this volume). The Iberian lynx (*Lynx pardinus*) is similarly a specialized rabbit hunter and its distribution is limited by the distribution of its prey on the Iberian peninsula, where disease has greatly reduced rabbit populations and there has been extensive habitat loss (Ferreras *et al.*, Chapter 24, this volume). Their specializations, on prey and habitat, may expose felids to anthropogenic threat and environmental or climate change. The more generalist, widespread species may be more robust to these threats, but none is immune to them. Generally, less than 10% of cat ranges consist of protected areas (Nowell and Jackson 1996); it is clear that these emblematic and threatened predators often occur beyond the safety of reserves.

Felid ecology and diet

Much of the behavioural ecology of felids is reviewed by Macdonald *et al.* (Chapter 5, this volume) but, as a foundation, here we briefly summarize some fundamentals. The most direct interface between felids and their environment is their diet. Environmental factors such as rainfall, seasonality, and nutrient availability in the environment determine primary production and hence the biomass of prey species (e.g. Coe *et al.* 1976; East 1984). In turn, biomass and dispersion of prey species in the environment determines felid population size and density, population structure, and social behaviour (Carbone and Gittleman 2002; Karanth *et al.* 2004c; Macdonald *et al.*, Chapter 5, this volume; Miquelle *et al.*, Chapter 13, this volume). Prey biomass and dispersion also determine home range size and intraspecific home range overlap, with home range size and often overlap between conspecific ranges inversely correlated with prey biomass (Macdonald *et al.*, Chapter 5, this volume; Miquelle *et al.*, Chapter 13, this volume; O'Donoghue *et al.*, Chapter 25, this volume; Loveridge *et al.*, 2009b).

Carnivores forage optimally when they are able to predate upon the largest suitable prey species they can safely kill; thus for each felid species there is a modal mass (and spread of taxa) of prey eaten by each population. In addition, diet varies according to individual and species prey preferences, local prey species assemblages, temporal availability of prey, and presence of intra-guild competitors. Taking leopards as an example, their prey may vary from hares (*Lepus* spp.) to kudu (*Tragelaphus strepsiceros*). In Gabon, the leopards studied by Henschel *et al.* (2005) ate a broad spread of prey sizes, peaking at 5.1–50 kg and comprising mainly ungulates (Fig. 1.2). Hayward *et al.* (2006) summarize how the average leopard diet varies across five African and three Asian populations (Fig. 1.3).

Similarly, the diet of ocelots differs radically between nine sites (Fig. 1.4; Moreno *et al.* 2006). As is commonplace for carnivores, the profile of prey consumed varies not only between felid species, but may also vary within species between populations, localities, territories, individuals, years, and seasons. Where studies are sufficient, generalities emerge, as for leopard diet

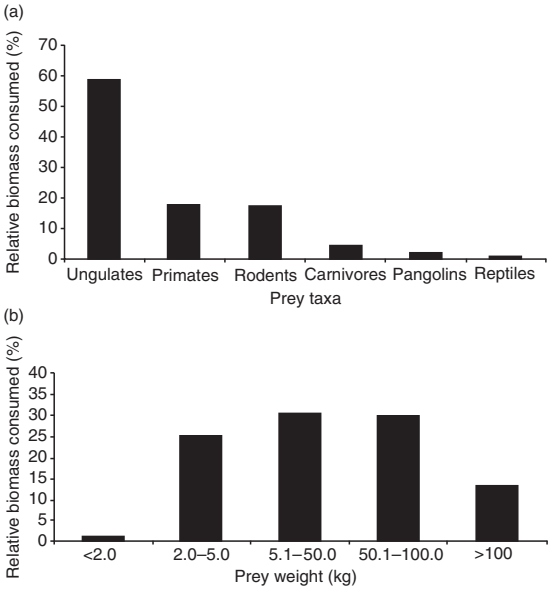


Figure 1.2 Representation of different (a) prey taxa; and (b) prey size classes in the diet of leopards. Calculations are based on a sample of 196 leopard scats, collected in the SEGC study area, Lopé National Park, Gabon, 1993–2001. (Taken from Henschel *et al.* 2005.)

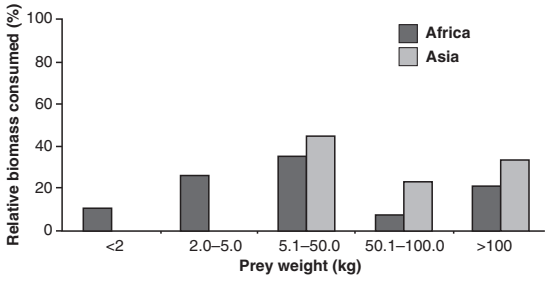


Figure 1.3 Total weight (kg) relative biomass consumed by African and Asian leopards. (Adapted from Hayward *et al*. 2006.)

from 41 localities (Fig. 1.5a), and for lions from 48 localities (Hayward and Kerley 2005) (Fig. 1.5b).

Diet may vary with season, over time, and with ecological conditions. In Patagonian Chile, Iriarte *et al*. (1991) analysed seasonal and yearly variation in puma diet between 1982 and 1988. Guanacos (*Lama guanicoe*) made up to 32% of prey items and accounted for 47% of the overall total biomass consumed by pumas. The proportion of guanaco remains in puma faeces increased from 9% to almost 30% of total prey items, paralleling an increase in the guanaco population from 670 to 1300 individuals in the study area.

Seasonality may affect populations differently, as illustrated by the patterns of prey availability experienced by the lions in the Serengeti plains and the nearby Ngorongoro Crater. Both have access to similar total annual prey biomass (12,000 kg/km^2; Hanby and Bygott 1987), but whereas this is resident in the Crater, on the plains it varies between 20,000 kg/km^2 in the wet season (November–May) and 1000 kg/km^2 in the dry season. Plains lions may have to switch to smaller, non-migratory prey in times of food shortage (Schaller 1972).

The proportion of prey species in the diet may differ from that in the environment due to various facets of their relative availability (such as size, habitat use, escape, and defensive behaviour), preference, or the impact of competitors (and even the size of the individual predator: juvenile puma eat smaller prey than do adults; Harveson 1997). Harveson *et al*. (2000) report that puma in southern Texas preyed on collared peccaries (*Pecari tajacu*) in proportion to their abundance, whereas by the same measure they selected for white-tailed deer (*Odocoileus virginianus*) and against feral hogs (*Sus scrofa*). Jaguars in Peru consumed collared peccary more frequently than expected, avoiding comparably abundant and similarly distributed white-lipped peccary and tapir (Emmons 1987; Weckel *et al*. 2006a, b).

In summary, the business of hunting is similar from the largest to the smallest felids. However, the relationship between the size of each felid species and that of its prey has reverberations throughout their behavioural ecology, and this is the topic of Macdonald *et al*. (Chapter 5, this volume).

Felid assemblages and communities

Intraspecific interactions

Most felids are solitary, with some notable exceptions (e.g. the lion, and to a lesser extent the cheetah, and wildcat). Conspecific interaction is generally limited to mating and the rearing of young (for females); when food is not scarce, a female cat is likely to be either pregnant or accompanied by dependent young (Sunquist and Sunquist 2002). However,

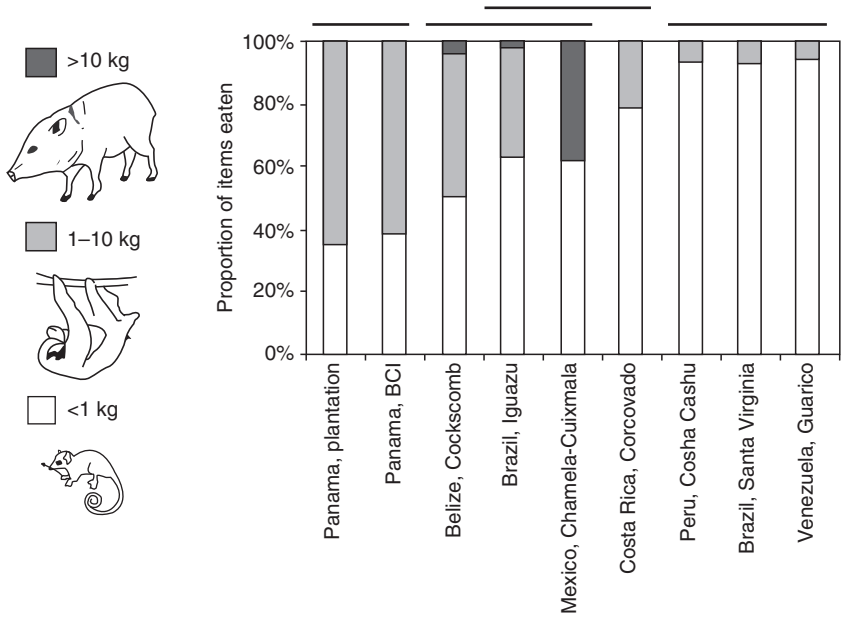


Figure 1.4 Weight of prey eaten by ocelots across nine sites. Top horizontal lines indicate the presence of robust sympatric jaguar populations. Horizontal lines above graph connect sites that are not significantly different from one another; distributions of prey size for all pairs of unconnected sites were significantly different (chi-square or Fisher's exact test on number of items detected in each size class, $P < 0.05$). *Sources*: Plantation and Barro Colorado Island (BCI), Panama (Moreno *et al.* 2006); Cockscomb, Belize (Konecny 1989); Iguazu, Brazil (Crawshaw 1995); Chamela-Cuixmala, Mexico (de Villa Meza *et al.* 2002); Corcovado, Costa Rica (Chinchilla 1997); Cosha Cashu, Peru (Emmons 1987); Santa Virginia, Brazil; and Guanico, Venezuela (Ludlow and Sunquist 1987). (Taken from Moreno *et al.* 2006.)

adults of some species collaborate in defence of territories, resources, mates, or offspring (Macdonald *et al.*, Chapter 5, this volume). Yet for many cats, conspecific encounters occur most frequently not between individuals, but between their signals, sent through territorial marking behaviour. Felids also compete for access to resources, ranges, mates, and/or reproductive opportunities, and deadly conspecific encounters have been recorded for some big cats. Among pumas, mature males may kill (but generally do not eat) other males (Anderson *et al.* 1992) or juveniles of both sexes (Harveson *et al.* 2000). Male African lions engage in combat for access to prides, and mortality among competing males is common (Schaller 1972). In Serengeti lions, adult female mortality rates are significantly correlated with the number of adult male neighbours, suggesting that females may be the target of attack by neighbouring males if they are not receptive to mating (Mosser 2008). However, for felids the most widely documented intraspecific mortality is infanticide, recorded for most pantherines (Davies and Boersma 1984; Bailey 1993; Smith 1993) and domestic cats (Macdonald *et al.* 1987; Macdonald *et al.*, Chapter 5, this volume). Typically, it is assumed to be by unrelated males, but Soares *et al.* (2006) speculated that the case of two jaguar cubs killed by their father was a pathology prompted by habitat fragmentation causing uncertainty over paternity.

Among lions, at a pride takeover, males famously either attack and kill, or otherwise cause the deaths of small cubs and evict larger ones they have not sired (Schaller 1972; Packer *et al.* 2001). Bertram (1975a) found a significant increase of mortality of lion cubs less than 24 months old in the first 4 months after a male takeover. (Of 11 takeovers there was only one in which small cubs survived.) Infanticide of tiger cubs is also associated with male territorial takeovers (Smith *et al.* 1987; Macdonald 1992). More than 50% of Serengeti lion cubs die

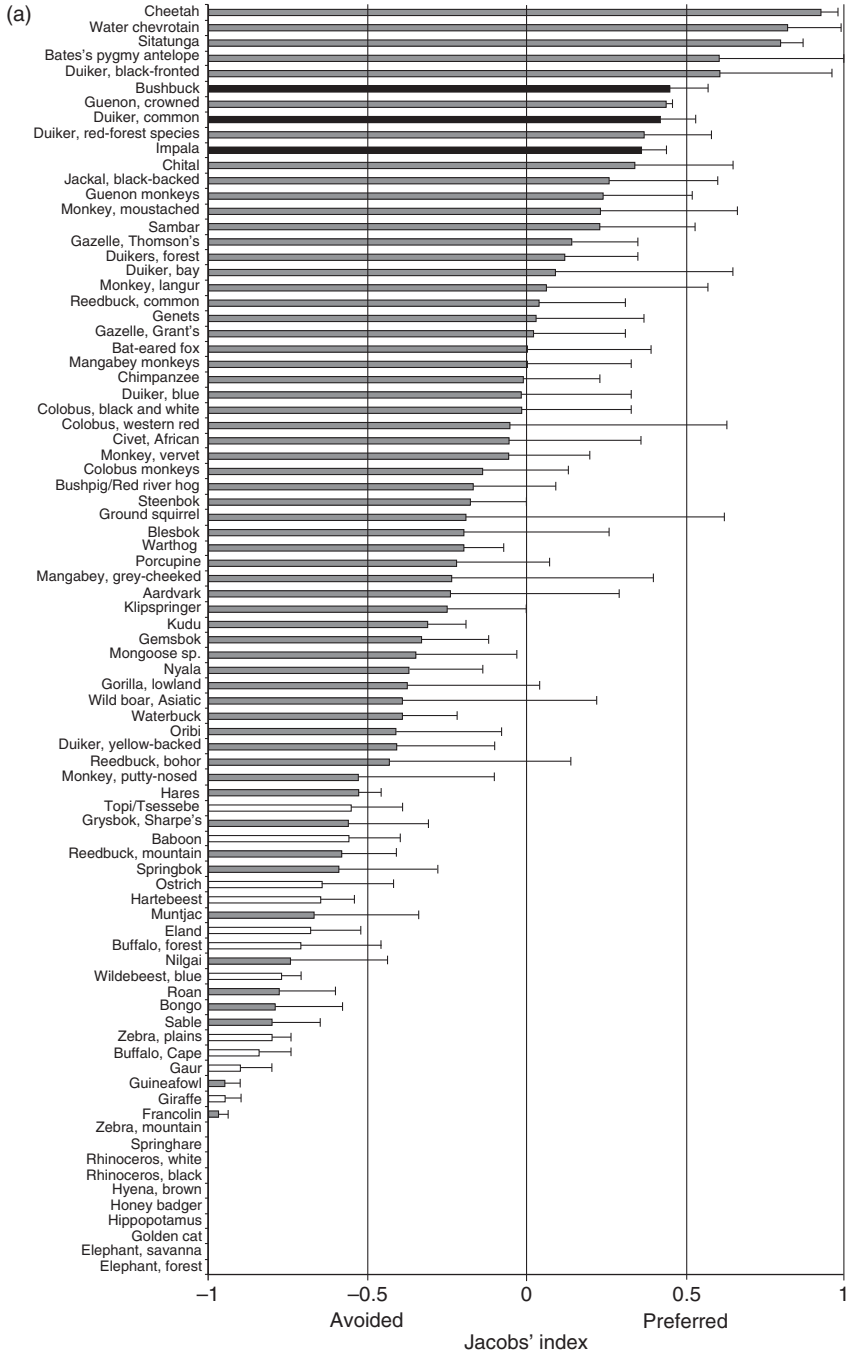


Figure 1.5 Dietary preferences determined with Jacob's index (mean ± 1 SE of species with >2 Jacob's index estimates) calculated for (a) leopards *Panthera pardus* from 41 populations; and (b) lions *Panthera leo* from 48 populations, all populations at differing prey densities for both species. Black bars represent species taken significantly more frequently than expected based on their abundance (preferred), grey bars indicate species taken in accordance with their relative abundance and unfilled bars show species taken significantly less frequently than expected based on their abundance (avoided). (Taken from Hayward *et al*. 2006a and Hayward and Kerley 2005.)

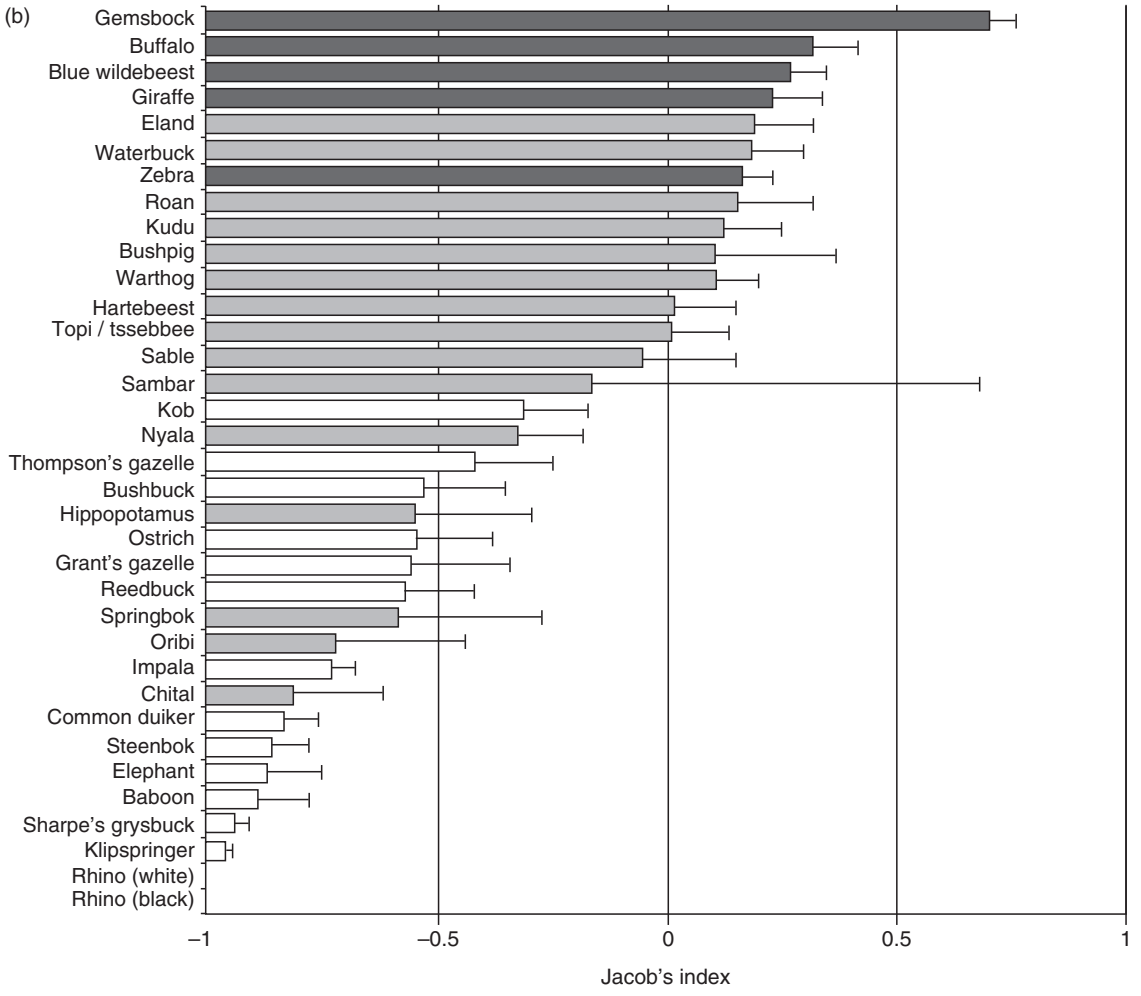


Figure 1.5 (Continued)

before their first birthday (Schaller 1972; Hanby and Bygott 1979) and females that lose their dependent offspring quickly resume mating activity, with the result that the synchronous loss of cubs at a takeover is followed by a synchronous resumption of mating activity. Consequently, the distribution of the duration of post-partum amenorrhoea across females reflects cub mortality for about the first 200 days after birth and reflects the approximate age of independence thereafter. Cubs have lower mortality when born synchronously (Bertram 1975) and mothers of single cubs are more likely to abandon them if they are born asynchronously than if they are born at the same time as other cubs in their pride (Rudnai 1974).

Community structure, interspecific relations, and intra-guild hostility

Interspecific competition is often a force that structures carnivore guilds and indeed widens communities of species (e.g. Rosenzweig 1966; Schoener 1974, 1984; Rautenbach and Nel 1978; Simberloff and Boecklen 1981). It is a phenomenon well described in the Canidae (Macdonald and Sillero-Zubiri 2004c), where interference competition by large canids has significant impacts on the distribution, density, and behaviour of smaller species. More subtle evidence of competition in the form of morphological character displacement has also been recorded in

sympatric canid species (Van Valkenburg and Wayne 1994; Dayan *et al*. 1989). Some evidence for character displacement among the felids has also been found (Dayan *et al*. 1992). Kiltie (1988) examined jaw lengths in regional assemblages of felids and found that female jaw length was closely correlated with modal prey weight. Since felids use a killing bite to dispatch prey, species that feed upon larger prey should have concomitantly wider jaw gapes. Hence, jaw lengths (and probably other morphological parameters) appear to have evolved to maximize efficiency in handling and killing common prey species and to minimize overlap with adjacent-sized species within the assemblage. Evenness in distribution of jaw lengths in regional assemblages of felid species may possibly indicate partitioning of resources within the felid guild. Such even size ratios are particularly apparent among the large Neotropical felids (Kiltie 1984). While this may well be evidence of character displacement, jaw lengths could equally have evolved as a response to the size distributions of available prey. Intriguingly, for three pairs of sympatric species (jaguarundi, *Puma yagouaroundi* and margay, *Leopardus wiedii*; serval, *Leptailurus serval* and caracal, *Caracal caracal*; and Asiatic golden cat, *Pardofelis temminckii* and fishing cat, *Prionailurus viverrinus*) whose jaw lengths (and therefore presumably modal prey size) were indistinguishable; one of the pair was always dappled (spotted or striped) the other plain, which Kiltie (1988) suggested may be indicative of ecological differences (e.g. different requirements for crypsis, differing behaviours, or habitat use).

Being so similar in form and function, coexisting felids are destined to rivalry. This competition can take a number of forms, for instance exploitative competition where sympatric felids compete for resources, or more direct interference competition, where sympatric felids harass or kill non-conspecifics (Mills 1991). Competitive interactions can determine the presence or absence, abundance, behaviour, and distribution of carnivores within guilds of sympatric species.

Exploitative competition

Sympatric carnivores may have significant dietary niche overlap. Andheria *et al*. (2007) compared the diets of tiger (*Panthera tigris*), leopard (*P. pardus*), and dhole (*Cuon alpinus*) in Bandipur Tiger Reserve (India), each of which kill 11–15 species of vertebrate prey, but three abundant ungulate species provide 88–97% of the biomass consumed by each. Although there was some difference in emphasis (the largest ungulates, gaur *Bos gaurus* and sambar *Cervus unicolor*, provided 63% of biomass consumed by tigers, whereas medium-sized chital *Axis axis* and wild pig *Sus scrofa* formed, respectively, 65% of the biomass intake of leopards) (Fig. 1.6), dietary niche overlap among the three species was high (Pianka's index of 0.75–0.93) and one species, chital, comprised 33% of tiger diet and 39% of leopard diet. Similarly, high dietary overlap between tigers and leopards (Pianka's index of 0.97) was found by Wang and Macdonald (2009) in Jigme Singye Wangchuck National Park, Bhutan, though overlap was less marked between these felids and dholes (Pianka's index of 0.58 and 0.66 for tigers/dholes and leopards/dholes, respectively).

Similarly, the diets of lions, leopards, and cheetahs all overlapped by species and size in Mala Mala (RSA), but the distributions of size classes (relative to the predators' body sizes) were significantly different (Radloff and du Toit 2004). Depending on the perspective, one might be impressed by the niche separation or its overlap: considering the cline in weights from lions (male 188 kg, female 124 kg), leopards (male 61.3 kg, female 37.3 kg), and cheetahs (male 53.9 kg, female 43.0 kg), it is noteworthy that only the three heaviest cats kill buffalo or zebra. The mean weights of kudus killed are 193, 165, 100, 88.9, 110, and 57.8 kg, respectively; it is also noteworthy that they all eat kudu (albeit in neatly graded mean sizes)! Bertram (1979) found little evidence of

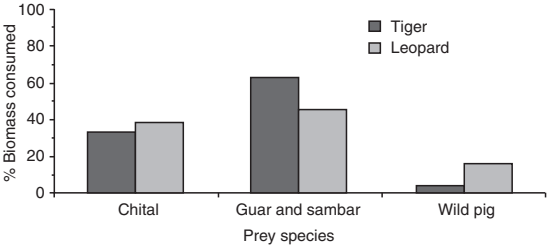


Figure 1.6 Percentage biomass consumed of different prey species by the tiger and leopard in the Bandipur Tiger Reserve, India. (Adapted from Andheria *et al.* 2007.)

exploitative competition among large felid species in the Serengeti, largely because they utilized prey of different sizes and employed different hunting techniques to capture prey. Pumas and jaguars are estimated to have a dietary overlap of up to 82% (Oliveira 2002). In the Paraguayan Chaco, jaguar and puma diet overlapped significantly in areas developed or over-exploited by people; however, in more pristine areas there was evidence of niche separation, with jaguars eating larger prey (Taber *et al.* 1997).

These wide niche overlaps may influence the choice of prey, behaviour, and distribution of the predators. For example, cheetahs unsurprisingly avoid lions, seeking out 'competition refuges' (Durant 2000a) and leopards allow tigers' first choice of habitats and prey (Eisenberg and Lockhart 1972; Seidensticker 1976a; but see Karanth and Sunquist 2000). Where there is a choice, leopards utilize smaller prey than do tigers (Karanth and Sunquist 1995). In Belize, female jaguars and male pumas overlap in size, suggesting the potential for competition. Camera-trapping data reveal that while activity patterns are similar, avoidance in space and time may minimize competitive interactions between the species (Harmsen *et al.*, Chapter 18, this volume). Schaller and Crawshaw (1980) found similar spatio-temporal avoidance between these species in the Brazilian Pantanal.

Absence or removal of larger competitors can result in competitive release for smaller species. In South America, margay, jaguarundi, oncilla (*Leopardus tigrinus*), and Geoffroy's cat (*L. geoffroyi*), occur at higher densities in the absence of larger ocelots, suggesting that ocelots may compete directly or indirectly with the smaller cats. However, ocelot numbers do not appear to be affected by the presence of much larger pumas or jaguars (Oliveira *et al.*, Chapter 27, this volume). In southern Africa, cheetah numbers are often higher on ranch lands where lions or spotted hyena have been extirpated than in protected areas, suggesting competitive release in the absence of larger competitors (Purchase and Vhurumuku 2005; Marker *et al.*, Chapter 15, this volume). Black-footed cats and African wild cats may benefit from the removal of larger competitors such as caracals and jackals (*Canis mesomelas*) (Sliwa *et al.*, Chapter 26, this volume).

Interference competition and intra-guild predation

The best-documented cause of interspecific mortality is intra-guild aggression (Wozencraft 1989; Palomares and Caro 1999). This peaks with 68% of cheetah cubs killed by lions, spotted hyenas, and leopards (Laurenson 1994, 1995b; Kelly and Durant 2000), and lions have negative impacts on the survival of females (Durant *et al.*, Chapter 16, this volume). Between 12% and 62% of bobcats (*Lynx rufus*) are killed by coyotes (*Canis latrans*) and pumas (Knick 1990; Koehler and Hornocker 1991), and 8% of lion cubs succumb to leopards and spotted hyenas (*Crocuta crocuta*) (Schaller 1972). In the Kalahari National Park, cheetahs lose competitive interactions with lions. However, lions had little effect on leopards and leopards did not affect cheetahs (Mills 1991). By contrast, in Hwange National Park a leopard was recorded killing and partially eating a cheetah (Davison 1967), G. Mills (personal communication) records similar behaviour in the Kalahari National Park (Fig. 1.7), and lions have been observed chasing leopards (A.J. Loveridge, personal observation). Perhaps the most extreme interspecific interaction is intra-guild predation. African leopards have been recorded as eating African golden cats, *Caracal aurata*, in central Africa (Henschel *et al.* 2005) and caracal in southern Africa (Hwange National Park; B. du Preez, personal communication). Caracals have been observed killing and partly eating African wildcats (G. Mills, personal comunication; Fig. 1.8). Leopards and pumas living in proximity to human settlements have a proclivity for predation on domestic cats (*Felis catus*; Martin and de Meulenaer 1988; Onorato *et al.*, Chapter 21, this volume).

Felids are part of wider carnivore guilds and interspecific competition is not limited only to sympatric felids. The interesting question is whether intra-family hostility is more punishing than inter-family competition. African wild dogs (*Lycaon pictus*) and dholes go out of their way to harass leopards (Davison 1967; Macdonald and Sillero-Zubiri 2004c;

Figure 1.7 A cheetah, killed and partly eaten by a leopard in the Kalahari. Circumstantial evidence indicated that the cheetah was injured prior to being attacked by the leopard. © M.G.L. Mills.

Figure 1.8 A caracal, having killed a wildcat, and carried it aloft a tree, in the Kalahari, prior to partly eating it. © M.G.L. Mills.

Venkataraman and Johnsingh 2004), perhaps because leopards not only compete for prey but also predate on adults and juveniles of these species. Spotted hyenas kleptoparasitize leopard kills and as a consequence leopards often cache their kills in trees out of reach of competitors. Lions and spotted hyenas compete fiercely for carcasses (Cooper 1991), and kill vulnerable adults and unprotected juveniles of the other species (A.J. Loveridge, personal observation).

Interactions with people: anthropogenic threats and conservation

The purpose of this book is twofold; first, to provide a compendium of knowledge on the biology of wild felids; second, to set that knowledge in the context of felid conservation, and to discuss how it can be used to greatest effect to safeguard their survival. These two purposes are each worthwhile in themselves, and

in the concluding synthesis (Macdonald *et al.*, Chapter 29, this volume) we will explore the inextricable linkages between them. However, to set the scene we will briefly summarize here some of the threats posed by people to wild felids, and vice versa.

Anthropogenic mortality, human–wildlife conflict, prey depletion, and habitat loss

Mortality comes in diverse guises, but the contemporary reality for several felid species may be that humans are either inadvertently (e.g. road traffic accidents, Haines *et al.* 2006) or deliberately (e.g. hunting, Altrichter *et al.* 2006) behind much of it (Loveridge *et al.*, Chapter 6, this volume). Anthropogenic mortality (including vehicle collisions) predominated among adult Eurasian lynx, with starvation, intra- and interspecific killing, and disease having a minor role (Andrén *et al.* 2006). Six of a sample of 15 radio-collared adult bobcats died, leading Fuller *et al.* (1985) to suggest that in many areas, sources of mortality other than legal trapping or hunting (e.g. poaching, starvation, disease, and predation), may be substantial (53% of all deaths for studied populations) and should be incorporated into models of bobcat population change. The composite demographic data from radio-telemetry field studies indicate that if populations are stable when adult survival is about 60% (40% mortality), and about 50% of mortality is not harvest related, then on average, harvests averaging over about 20% of the population (40% mortality $\times$ 0.5) will be likely to result in declining populations. Of course, harvests of <20% of the population may also cause a decline if the rates of natural mortality are high, or if reproductive success is low. Annual losses to tiger populations in the Russian Far East that exceed 15% are predicted to lead to population declines (Chapron *et al.* 2008a).

A global craze for spotted cat fur coats in the 1960s was the genesis of the Convention on International Trade in Endangered Species (CITES), which regulates international trade (Nowell and Jackson 1996). Although some harvest and trade is well managed and legal, poaching and illegal trade for skins and body parts may present both a significant cause of mortality and a conservation threat for target species (Loveridge *et al.*, Chapter 6, this volume; Damania *et al.* 2008). Illegal trade in wildlife is not only increasing in magnitude, but is thought to be the second largest area of organized crime after the illegal drug trade (Angulo *et al.* 2009). Many of the felid species that feature in illegal trade, such as the tiger and other Asian cats are already rare and facing threats to their survival through habitat loss and isolation of existing populations (Rabinowitz 1999). The concern is that the demands of the illegal market may overwhelm the attempts of conservationists to protect these species in the wild unless international action is taken to curb trade.

In many cases, anthropogenic mortality is linked to conflict with people over space, depredation of livestock or game animals, and occasionally over man-eating incidents (Loveridge *et al.*, Chapter 6, this volume; Breitenmoser *et al.*, Chapter 23, this volume). Livestock owners, game farmers, and bereaved communities often respond to depredations (and other conflict situations) by poisoning, trapping, or shooting the predators responsible. Such control measures can be legal and well controlled or illegal and uncontrolled, the later potentially leading to population declines or extirpation.

Human activity can also indirectly impact felids by depletion of prey species populations. Carnivore population size is closely linked to abundance of prey species, therefore depletion of the prey base can have catastrophic impacts on felid populations (Karanth *et al.* 2004a). The bushmeat trade in some areas of central Africa has resulted in 'empty forest syndrome' where, although habitat has remained relatively intact, medium- to large-sized mammalian species have been decimated by over-hunting. Under these conditions, the prey base cannot support viable populations of species such as leopards (Henschel 2007).

However, one of the greatest threats to felids and biodiversity as a whole is loss of natural habitats: a global trend the rate of which is predicted to accelerate into the next millennium (Millennium Ecosystem Assessment 2005). Conversion of natural habitat to agricultural land and linked loss of natural prey is a major threat to all felid species and one that might be expected to cause the demise of many populations if present trends are not halted. Salvation may lie in continued protection of existing protected areas and creation of corridors that link these together (Weber and Rabinowitz 1996; Macdonald *et al.*, Chapter 29, this volume).

Conservation of felids

The IUCN Red List of Threatened Species (IUCN 2008) is considered to be the most authoritative index of species status, particularly for mammals, which was recently reassessed in a massive global exercise (Schipper *et al*. 2008). Threat categories are assigned based on quantitative criteria, with thresholds for population size, range size, rate of decline, or probability of extinction (e.g. the Iberian lynx qualifies as Critically Endangered by having a fragmented, declining population of fewer than 250 mature individuals). Over 44% of felids (16 of 36 species) are included in the top three categories of threat (Critically Endangered, Endangered, and Vulnerable) with an elevated extinction risk (Table 1.2). While larger mammals are significantly more threatened than small mammals, felids are not significantly more threatened than expected, although their threat level is relatively high compared to carnivores and mammals in general (25% of both groups being in

Table 1.2 Conservation status of cat species on the 2008 IUCN Red List of Threatened Species.

Critically Endangered
Extremely high extinction risk
Iberian lynx *Lynx pardinus*

Endangered
Very high extinction risk
Andean cat *Leopardus jacobita*
Tiger *Panthera tigris*
Snow leopard *Panthera uncia*
Borneo bay cat *Pardofelis badia*
Flat-headed cat *Prionailurus planiceps*
Fishing cat *Prionailurus viverrinus*

Vulnerable
High extinction risk
Cheetah *Acinonyx jubatus*
Black-footed cat *Felis nigripes*
Guiña *Leopardus guigna*
Oncilla *Leopardus tigrinus*
Sunda clouded leopard *Neofelis diardi*
Clouded leopard *Neofelis nebulosa*
Lion *Panthera leo*
Marbled cat *Pardofelis marmorata*
Rusty-spotted cat *Prionailurus rubiginosus*

Near Threatened
Close to qualifying for a higher threat category
African golden cat *Caracal aurata*
Sand cat *Felis margarita*
Pampas cat *Leopardus colocolo*
Geoffroy's cat *Leopardus geoffroyi*
Margay *Leopardus wiedii*
Pallas's cat *Otocolobus manul*
Jaguar *Panthera onca*
Leopard *Panthera pardus*
Asiatic golden cat *Pardofelis temminckii*

Least Concern
Relatively widespread and abundant
Caracal *Caracal caracal*
Jungle cat *Felis chaus*
Wildcat *Felis silvestris*
Ocelot *Leopardus pardalis*
Serval *Leptailurus serval*
Canada lynx *Lynx canadensis*
Eurasian lynx *Lynx lynx*
Bobcat *Lynx rufus*
Leopard cat *Prionailurus bengalensis*
Puma *Puma concolor*
Jaguarundi *Puma yagouaroundi*

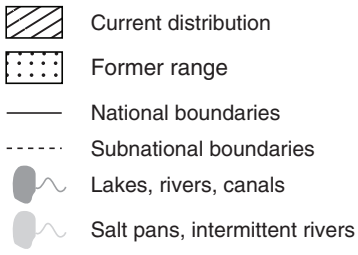
the top three categories; Schipper *et al.* 2008). Dividing felids into eight clades (Werdelin *et al.*, Chapter 2, this volume) reveals that for three lineages the majority of species are threatened (*Panthera, Pardofelis*, and leopard cat lineages). Most of this group occurs in south and south-east Asia, as do threatened mammals in general (Schipper *et al.* 2008), although the only Critically Endangered felid, the Iberian lynx, occurs in Europe (Spain). The other species in its clade are classified as Least Concern, demonstrating that extinction risk is uneven across the remaining lineages. An additional 20 subspecies are included in the top three categories, although not all felid subspecies have yet been assessed. Leading threats to felids are similar to those found for mammals in general, being primarily habitat loss and degradation, followed by hunting pressure (Schipper *et al.* 2008).

Historically, wild felids have been hunted and persecuted (Tuck 2005), but also valued and revered (Callou *et al.* 2004). This dichotomy continues to be reflected in contemporary interactions between people and wild cats. On the one hand, tourists are enthralled by sightings of large free-ranging cats in national parks around the world while, beyond protected areas, rural people suffer depredations from the same species. Westerners may desire the conservation of the toothed and clawed creatures brought to the safety of their living rooms by television programmes, but living with large wild felids is anything but easy. The cultural and aesthetic values some people accord to charismatic species are often at odds with the conflict between them and the people who live with them. These issues are explored in Macdonald *et al.* (Chapter 29, this volume). Mechanisms for ameliorating this conflict include zonation and protection of wild habitats, compensation and protection of livelihoods, as well as integration of local communities into conservation activities and revenue-generating ecotourism.

Dramatis personae

Felid systematics have been well studied, but a consensus taxonomy, especially concerning the number of genera, has been slow to emerge. Speciation events have been relatively rapid and recent in the family, resulting in a sparse fossil record and few distinguishing morphological characteristics (Johnson *et al.* 2006b). Species vignettes are presented here following the recent well-supported revised classification of the Felidae based on molecular analysis of nuclear and mitochondrial DNA (Johnson *et al.* 2006b; O'Brien and Johnson 2007; Eizirik *et al.*, in prep; Werdelin *et al.*, Chapter 2, this volume). This taxonomic arrangement is in general agreement with other recent authorities (e.g. Wozencraft 2005; Macdonald 2006). Some notable differences include two species of clouded leopard (*Neofelis nebulosa* and *N. diardi*), one species of pampas cat (*Leopardus colocolo*), and the Chinese mountain cat as a subspecies of wildcat (*Felis silvestris bieti*).

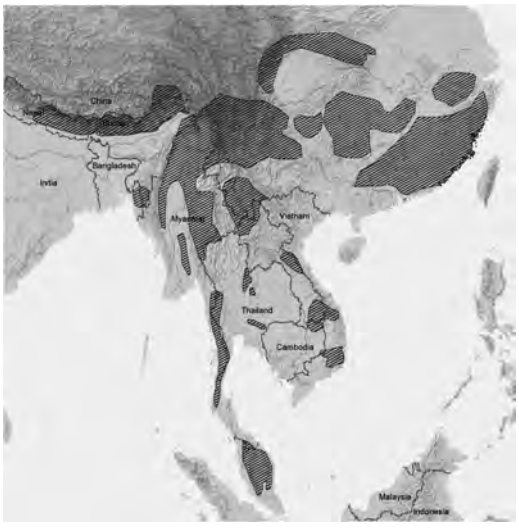
Box 1.1 Legend for species distribution maps



Source: All maps from the IUCN Red List of Threatened Species. © IUCN 2008.

Clouded leopard *Neofelis nebulosa* (Griffith, 1821)

The clouded leopard, named for its elliptical pelage markings, held the unique position within the family Felidae of a 'small, big cat' (Sunquist and Sunquist 2002) until it was split into two species in 2006 (see *Neofelis diardi*). Both are now placed with the genus *Panthera* in the tribe Pantherini (Eizirik *et al.*, in prep). The skulls of clouded leopards are reminiscent of sabre-toothed machairodonts, their upper canine teeth being longer, relative to skull length, than those of any extant big cat (Christiansen 2006); measuring 3.8–4.5 cm (Guggisberg 1975). It is highly arboreal, its tail being *c.* 1 m long, although clouded leopards have been most frequently observed on the ground (Sunquist and Sunquist 2002). While they have been observed hunting primates in trees (Nowell and Jackson 1996), the only study to



Map 1 Clouded leopard. © IUCN Red List 2008.

overlap between males and females, Grassman *et al.* (2005b) also reported 39% overlap in the ranges of two males. Illegal trade is a serious threat, with large numbers of skins (largely of wild provenance) seen in markets, as well as bones for medicines, meat for exotic dishes, and live animals for the pet trade (Nowell 2007).

	Male		Female	
	Mean	Sample size	Mean	Sample size
Weight (kg)	16–18	$n = 2$	11.5–13.5	$n = 2$
Head/body length (mm)	980–1080	$n = 2$	820–940	$n = 2$

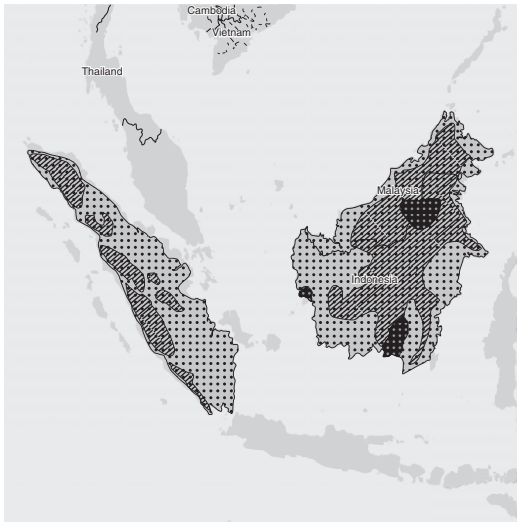
Refs: Austin and Tewes (1999); Grassman *et al.* (2005b)

examine diet found hog deer (*Axis porcinus*), Asiatic brush-tailed porcupine (*Atherurus macrourus*), Malayan pangolin (*Manis javanica*), and Indochinese ground squirrel (*Menetes berdmorei*) (Grassman *et al.* 2005b). The clouded leopard, classified as Vulnerable (IUCN 2008), is found from the Himalayan foothills in Nepal through mainland south-east Asia into China (Map 1), where it has suffered heavy range loss (not shown on Map 1), and is extinct on Taiwan (Anonymous 1996). Although strongly associated with primary evergreen tropical rainforest, there are records from dry and deciduous forests, and secondary and logged forests. They have been recorded in the Himalayas up to 2500 m and possibly as high as 3000 m. Less frequently, they have been found in grassland and scrub, dry tropical forests, and mangrove swamps (Nowell and Jackson 1996). Radiotracking in Thailand revealed a preference for forest (Austin *et al.* 2007), with both sexes occupying similar-sized home ranges of 30–40 km^2 (95% fixed kernel estimators) with intensively used core areas of 3–5 km^2 (Grassman *et al.* 2005b; Austin *et al.* 2007). Clouded leopards in Phu Khieu National Park travelled approximately twice the average daily distance (average 2 km: Grassman *et al.* 2005b) than those in Khao Yai National Park (Austin *et al.* 2007). While both studies found substantial home range

Sunda clouded leopard *Neofelis diardi* (Cuvier, 1823)

The genetic differences between the Sunda clouded leopard and *N. nebulosa* are greater than those between well-accepted *Panthera* species (Buckley-Beason *et al.* 2006), and its pelage has smaller cloud-like markings (Kitchener *et al.* 2006). It is restricted to the islands of Sumatra and Borneo (Kitchener *et al.* 2007; Wilting *et al.* 2007a; Map 2). Analysis of mitochondrial DNA sequences suggests the Sumatran and Bornean populations deserve recognition at the subspecies level, and have been isolated from each other since the middle to late Pliocene (2.86 million years ago) (Wilting *et al.* 2007b). Like the mainland clouded leopard, it is highly arboreal. Holden (2001) found that on level or undulating terrain clouded leopards were seldom if ever caught on camera traps, suggesting considerable arboreality, although their spoor is recorded along logging roads and trails (Holden 2001; Gordon and Stewart 2007). Clouded leopards may be less arboreal on Borneo (Rabinowitz *et al.* 1987) than on Sumatra, where tigers and leopards are sympatric. They may also occur at higher densities: 6.4 adults (A. Hearn and J. Ross, personal communication in IUCN 2008) to 9.0 adults/100 km^2 (Wilting *et al.* 2006) on Borneo, compared to 1.29/100 km^2 on Sumatra (Hutajulu *et al.*

Plate A Sunda clouded leopard *Neofelis diardi*, caught on a camera trap. © Andreas Wilting.



Map 2 Sunda clouded leopard. Former range coincides with areas where forest cover has been largely lost (GLC 2000, S. Cheyne, personal communication 2008). © IUCN Red List 2008.

2007). They are classified as Vulnerable by IUCN (2008). The Sumatran province of Riau lost 11% of its forest cover in 2005/6, and 65% over the past 25 years (Uryu *et al*. 2008), and if deforestation continues apace Borneo could lose its lowland forests by 2012–2018 (Rautner *et al*. 2005).

	All (range)
Weight (kg)	11–20
Head/body length (mm)	600–1000
Ref: Macdonald (2001a)	

Lion *Panthera leo* (Linnaeus, 1758)

Lions are uniquely social among wild felids, living in prides of up to 18 adult females and 1–9 adult males. Male lions are also unique for their dark manes, which are protective and signal fitness (West and Packer, in press). Lions occur at 1.2 adults/100 km^2 in southern African semi-desert to 40/100 km^2 in the Ngorongoro Crater, Tanzania (Hanby *et al*. 1995;

Map 3 Lion. © IUCN Red List 2008.

Castley *et al*. 2002). Pride ranges can vary widely even in the same region: for example, from 266 to 4532 km^2 in the Kgalagadi Transfrontier Park of South Africa (Funston 2001a), and 20–500 km^2 in the Serengeti (West and Packer, in press). Females do most of the hunting, and all pride members generally share the carcass, typically a large ungulate (Scheel and Packer 1995), although lions can and often do live on small prey (Sunquist and Sunquist 2002). Lion sociality is flexible, prides being smaller when persecuted by humans (Funston *et al*. 2007). In the more arid habitats of southern Africa, pride sizes are also smaller (West and Packer, in press), and in India's Gir Forest, males and females infrequently associate (Chellam 1993). The Gir Forest lions (*P. l. persica* ssp.: O'Brien *et al*. 1987b) are the only remaining population (estimated at ~175: IUCN 2008) in the wide historic Asian range of the lion. The Gir National Park and Wildlife Sanctuary is surrounded by cultivated areas and inhabited by pastoralists (Maldharis) and their livestock. Domestic cattle have historically been a major part of the Asiatic lion's diet, although the most common prey is the chital deer (Nowell and Jackson 1996). Outside this isolated Indian population, the lion is now found only south of the Sahara, primarily in savannah habitats, and primarily in eastern and southern Africa (77% of current lion range; Map 3). Lion status in 38% of its historic range is unknown, and known and probable range comprises just 22% of historic range (IUCN 2006a, b). The lion is considered regionally Endangered in west Africa (Bauer and Nowell 2004). The African lion population has been estimated at 23,000 (Bauer and van der

Plate B A male and a female lion (*Panthera leo*) in Hwange National Park, Zimbabwe, showing the marked sexual dimorphism characteristic of the species. © A. J. Loveridge.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)						
East Africa[ab]	173.9	145.4–204.7	*n* = 27	117.7	90.0–167.8	*n* = 15
Southern Africa[b]	189.6	150.0–225.0	*n* = 78	103.8	83.0–165.0	*n* = 118
Head/body length (mm)						
East Africa[a]	1938	1840–2080	*n* = 12	1711	1600–1840	*n* = 38
Southern Africa[c]	1949	1835–2090	*n* = 18	1710	1425–1850	*n* = 23

Refs: [a] West and Packer (in press); [b] Smuts *et al*. (1980); [c] A. Loveridge (unpublished data)

Merwe 2004) and 39,000 (Chardonnet 2002). An estimated 42% of major lion populations are declining (Bauer 2008). Genetic population models indicate that large populations (50–100 lion prides) are necessary to conserve genetic diversity and avoid inbreeding, which increases significantly when populations fall below 10 prides. Male dispersal is also important to conserving genetic variation (Björklund 2003). These conditions are rarely met, although there are at least 17 lion 'strongholds' >50,000 km^2 (Bauer 2008). The major threat facing lions is conflict with local people over life and livestock (IUCN 2006b). The lion is classified as Vulnerable, the Asiatic lion as Endangered (IUCN 2008).

Jaguar *Panthera onca* (Linnaeus, 1758)

The largest cat of the Americas, the jaguar is similar in appearance to the leopard *P. pardus*, but with a stockier build, more robust canines, and larger rosettes. Historically, the jaguar ranged from the south-western United States (where there are still some vagrants close to the Mexican border: Brown and Lopez-Gonzalez 2001) south through the Amazon basin to the Rio Negro in Argentina. It has been virtually eliminated from much of the drier northern parts of its range, as well as northern Brazil, the pampas scrub grasslands of Argentina, and throughout Uruguay, losing 54% of its historic range. However, it has high probability of survival in 70% of its current range (Map 4), comprised mainly of the Amazon basin rainforest, and adjoining areas of the Pantanal and Gran Chaco (Sanderson *et al*. 2002b). However, while ecological models suggest that the latter two are highly suitable for jaguars, the Amazon may be less so (Torres *et al*. 2007). Jaguar densities in the Brazilian Pantanal are estimated at 6.6–6.7 adults/100 km^2 (Soisalo *et al*. 2006), and in the Bolivian Gran Chaco 2.2–5/100 km^2 (Maffei *et al*. 2004a). In the Amazon basin in Colombia, jaguar density was estimated at 4.5/100 km^2 in Amacayacu National Park and 2.5/100 km^2 in unprotected areas (Payan 2008). In Madidi National Park in the Bolivian Amazon, density was estimated at 2.8/100 km^2 (Silver *et al*. 2004). Areas of tropical moist lowland forest in Central America also have high probability for long-term jaguar persistence (Sanderson *et al*. 2002b); density in Belize was estimated at 7.5–8.8/100 km^2 (Silver *et al*. 2004). Small home ranges were also reported there, with females averaging

Map 4 Jaguar. © IUCN Red List 2008.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	104.5	68–121	$n = 26$	66.9	51–100	$n = 31$
Head/body length (mm)	1565	1260–1700	$n = 16$	1304	1160–1470	$n = 12$

Source: Hoogesteijn and Mondolfi (1996).

10 km^2 and males averaging 33 km^2, and extensive intra- and intersexual overlaps (Rabinowitz and Nottingham 1986). Larger home ranges for both males and females, up to ~150 km^2, have been reported elsewhere (Sunquist and Sunquist 2002). More than 85 prey species have been recorded, although large ungulates are preferred (Seymour 1989). People compete with jaguars for prey, and jaguars are frequently shot on sight, despite protective legislation (Nowell and Jackson 1996). An estimated 27% of jaguar range has a depleted wild prey base (WCS 2008). An ambitious programme is seeking to conserve a continuous north-to-south corridor through the species range (Rabinowitz 2007). The jaguar is classified as Near Threatened (IUCN 2008), but some of the most important Jaguar Conservation Units occur where their probability for long-term survival is low (Sanderson *et al*. 2002b). These include the Atlantic Forest subpopulation in Brazil, estimated at 200 ± 80 adults (Leite *et al*. 2002). Jaguar populations in the Chaco region of northern Argentina and Brazil, and the Brazilian Caatinga, are low density and highly threatened by livestock ranching and persecution (Altrichter *et al*. 2006; T. de Oliveira, personal communication 2008).

Leopard *Panthera pardus* (Linnaeus, 1758)

With a distribution that includes most of Africa and large parts of Asia (Map 5), ranging from desert to rainforest, the leopard is adaptable and widespread, but many subpopulations are threatened. In Africa, they are most successful in woodland, grassland savannah, and forest, but also occur widely in mountain habitats (up to 4600 m), coastal scrub, swampy areas, shrubland, semi-desert, and desert—although they have become very rare in the areas bordering the Sahara (Ray *et al*. 2005; Hunter *et al*., in press). In south-west and central Asia, leopards are now confined chiefly to the more remote montane and rugged foothill areas (Breitenmoser *et al*. 2006a, 2007). Through India and south-east Asia, they occur in all forest types as well as dry scrub and grassland, and range up to 5200 m in the Himalaya (Nowell and Jackson 1996). Over 90 species have been recorded in leopard diet in sub-Saharan Africa, ranging from arthropods to adult male eland *Tragelaphus oryx* (Hunter *et al*., in press). Preferred prey in Thailand were hog badger *Arctonyx collaris* (45.9% of prey items), muntjac *Muntiacus muntjak* (20.9%), and wild pig *Sus scrofa* (6.3%; Grassman 1998a). Densities vary with habitat, prey availability, and degree of threat, from fewer than 1/100 km^2 to over 30/100 km^2, with highest densities obtained in protected east and southern African mesic woodland savannahs (Hunter *et al*., in press). Home ranges

Map 5 Leopard. © IUCN Red List 2008.

Plate C A male African leopard (*Panthera pardus*), Hwange National Park, Zimbabwe. © A. J. Loveridge.

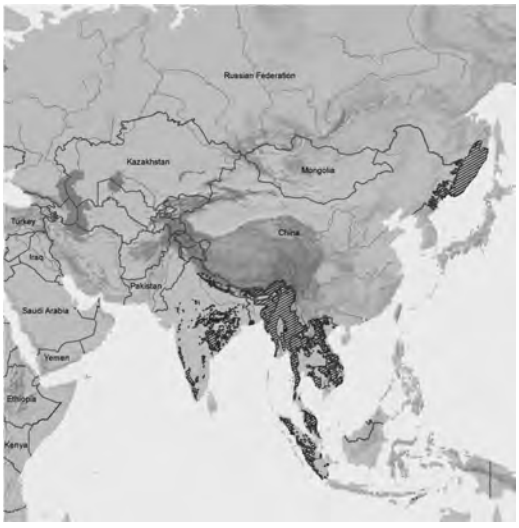
	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	53	34–69	*n* = 59	30.5	20.5–42	*n* = 58
Head/body length (mm)	1340	1160–1830	*n* = 59	1143	1050–1270	*n* = 58

Source: Hunter *et al*. (in press).

from two studies in Thailand were 8.8 km^2 (Grassman 1998a) and 11–17 km^2 (Rabinowitz 1989) for females, and 17.3–18 km^2 (Grassman 1998a) and 27–37 km^2 for males (Rabinowitz 1989). The major threats to leopards are habitat loss, prey base depletion, illegal trade in skins and other body parts, and persecution in retribution for real and perceived livestock loss (IUCN 2008). The leopard is classified as Near Threatened, with five genetically distinct subspecies (Miththapala *et al*. 1996; Uphyrkina *et al*. 2001) included on the IUCN Red List. *P. p. melas* (Java), *P. p. nimr* (Arabia), and *P. p. orientalis* (Russian Far East) are Critically Endangered, and *P. p. kotiya* (Sri Lanka) and *P. p. saxicolor* (eastern Turkey, the Caucasus Mountains, northern Iran, southern Turkmenistan, and parts of western Afghanistan) are Endangered (IUCN 2008).

Tiger *Panthera tigris* (Linnaeus, 1758)

The tiger is the largest felid (much larger in India and Russia than in south-east Asia; Kitchener 1999) and the only striped cat. Genetic analysis supports five classically described subspecies—*P. t. altaica* in the Russian Far East; *P. t. amoyensis* in South China (now possibly extinct in the wild; IUCN 2008); *P. t. corbetti* in south-east Asia; *P. t. sumatrae* on the Indonesian island of Sumatra; and *P. t. tigris* on the Indian subcontinent—as well as a new subspecies, *P. t. jacksonii*, restricted to Peninsular Malaysia (Luo *et al*. 2004). Tigers once ranged from Turkey in the west to the eastern coast of Russia (Nowell and Jackson 1996). Over the past 100 years tigers have disappeared from south-west and central Asia, from two Indonesian islands (Java and Bali) and from large areas of south-east and eastern Asia, and lost 93%



Map 6 Tiger. © IUCN Red List 2008.

of their historic range (Sanderson *et al.* 2006). Comparison of current range (~1.1 million km^2; Sanderson *et al.* 2006; Map 6) with an estimate a decade ago (Wikramanayake *et al.* 1998) suggests 41% shrinkage. While partly due to methodological distortions (Karanth *et al.* 2003; Sanderson *et al.* 2006), Dinerstein *et al.* (2007) consider tiger poaching and habitat loss to have caused major recent decline. The global population is only *c.* 3500–5000 tigers (IUCN 2008), compared to previous estimates of 5000–7000 (Seidensticker *et al.* 1999), although such direct comparison is unreliable due to improved precision of recent estimates (e.g. Miquelle *et al.* 2007; Jhala *et al.* 2008). Sanderson *et al.* (2006) still consider 77% of current range to consist of 'known and secured breeding populations of tigers in areas large enough for a substantive population'. Most tiger range (60%) is found in tropical and subtropical moist broadleaf forests, followed by temperate and broadleaf mixed forest (21%) and tropical and subtropical dry broadleaf forest (10%). Tigers also occur in coniferous forest, mangrove forest, and tropical grass and shrubland (Sanderson *et al.* 2006). Photos of tigers at elevations up to 4500 m have been obtained in Bhutan (Wang 2008). Tigers depend on a large ungulate prey base (Sunquist *et al.* 1999), and are capable of killing prey as large as adult Asian rhinos and elephants (Sunquist and Sunquist 2002). Tigers eat 18–27 kg of food in a single feeding session (Schaller 1967), and up to 35 kg (McDougal 1977). In Nepal's Chitwan National Park, a female spent an average of 3 days with a large kill (Sunquist 1981). Karanth *et al.* (2004a) estimate that tigers need to kill 50 large prey animals per year. Tigers are generally solitary, with adults maintaining exclusive

Plate D Tiger *Panthera tigris*. © Brian Courtenay.

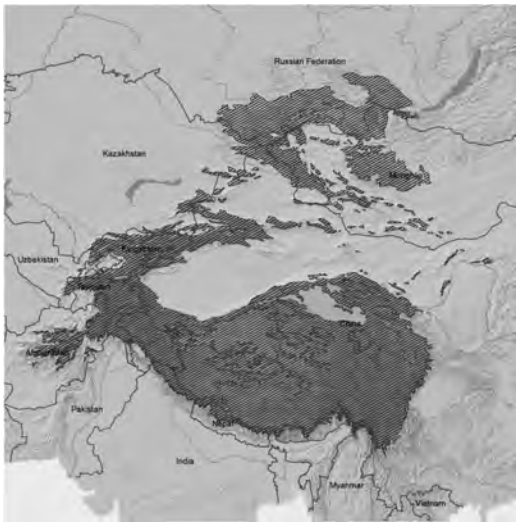
	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	225	195–325	$n = 9$	121	96–160	$n = 5$
Head/body length (mm)	2300	1900–2900	$n = 5$	1663	1460–1770	$n = 5$

Source: Heptner and Sludskii (1992)

territories, or home ranges. Adult female home ranges seldom overlap, whereas male ranges typically overlap from one to three females (Sunquist and Sunquist 2002). Tiger home ranges are small where prey is abundant—for example, female home ranges in Chitwan averaged 20 km^2 (Smith *et al.* 1987) and 15–20 km^2 in India's Nagarhole National Park (Karanth 1993), while in the Russian Far East they are much larger, at 400 km^2 (Goodrich *et al.* 2007). Male tiger home ranges are 2–15 times larger than females (Sunquist and Sunquist 2002), and average 1379 $\pm$ 531 km^2 in the Russian Far East (Goodrich *et al.* 2007). Similarly, reported tiger densities range from 11.65 adult tigers/100 km^2 where prey is abundant (India's Nagarhole National Park) to as low as 0.13–0.45/100 km^2 where prey is more thinly distributed, as in Russia's Sikhote Alin Mountains (Nowell and Jackson 1996). With their substantial food requirements, tigers require a healthy large ungulate prey base, but these species are also under heavy human subsistence hunting pressure and competition from domestic livestock. Karanth and Stith (1999) consider prey base depletion to be the leading threat to tigers in areas of otherwise suitable habitat. Tiger attacks on livestock and people lead to local conflict. For example, 41 people were killed by tigers in the Sundarbans mangrove forest of Bangladesh during an 18-month period in 2001–03 (Khan 2004). Tigers are also commercially poached, for their skins as well as bones, used in traditional Asian medicine, particularly in China. While China's 1993 trade ban has greatly reduced illegal trade there, there are proposals to farm tigers to make tiger bone wine. Five thousand tigers are reputedly already in captivity, and tiger farming threatens to re-ignite consumer demand (Nowell and Xu 2007; Nowell, 2009). In 2007, the CITES enacted a decision stating that 'tigers should not be bred for trade in their parts and derivatives' (Nowell *et al.* 2007). The tiger is classified as Endangered (IUCN 2008).

Snow leopard *Panthera uncia* (Schreber, 1775)

The snow leopard's closest relative is the tiger (Johnson *et al.* 2006b; O'Brien and Johnson 2007; Eizirk *et al.*, in press), and it is also classified as Endangered (IUCN 2008), with an estimated population of 4080–6590 (McCarthy and Chapron 2003). Status in China, which makes up a large portion of snow leopard range (see Map 7), is little known. Snow leopards are restricted to the high arid mountain grasslands of central Asia, at 3000 to over 5000 m in the Himalaya and Tibetan plateau, but as low as 600 m in Russia or Mongolia. In the Sayan Mountains of Russia and parts of the Tien Shan range of China, they are found in open coniferous forest, but usually avoid dense forest (McCarthy and Chapron 2003). With their pale colouration, thick fur, and long luxuriant tail, they are adapted for cold, snowy, and rocky environments. They may occur in sympatry with tigers or leopards at high elevations in the Himalaya



Map 7 Snow leopard. © IUCN Red List 2008.

Plate E Snow leopard *Panthera uncia* cubs. © Snow Leopard Conservancy.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	40.7	40–41.3	*n* = 2	34.3	30–38.6	*n* = 2
Head/body length (mm)	1210	1200–1220	*n* = 2	1173	1170–1175	*n* = 2

Source: McCarthy (2000)

(Wang 2008). Deep snow is not a barrier, although they prefer to use existing trails to avoid breaking through new snow (Sunquist and Sunquist 2002). The snow leopard's principal natural prey species are bharal or blue sheep (*Pseudois nayaur*) and ibex (*Capra sibirica*), which have a largely coincident distribution. They also take marmot (*Marmota* spp.), pika (*Ochotona* spp.), hares (*Lepus* spp.), small rodents, and game birds. Considerable predation is reported on domestic livestock. Annual prey requirements are estimated at 20–30 adult blue sheep, with radio-tracking data indicating such a kill every 10–15 days. Snow leopards may remain with their kills for up to a week. Snow leopard home ranges overlap widely between the sexes, and varied from 10 to 40 km^2 in relatively productive habitat in Nepal (Jackson and Ahlborn 1989). By comparison, home ranges are considerably larger (140 km^2 or greater) in Mongolia, where terrain is relatively open and ungulate prey densities lower (McCarthy *et al.* 2005). Densities range from 0.1 to 10 or more individuals/100 km^2 (Jackson *et al.*, Chapter 19, this volume). Major threats to the snow leopard include prey base depletion, illegal trade in skins and bones (used as a substitute for tiger bone medicine), conflict with local people, and lack of conservation capacity, policy, and awareness (Koshkarev and Vyrypaev 2000; McCarthy and Chapron 2003; Theile 2003).

Borneo bay cat *Pardofelis badia* (Gray, 1874)

The Borneo bay cat (Map 8) is not, as previously thought, a small island form of the Asiatic golden

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)				2.45	2.39–2.5	*n* = 2
Head/body length (mm)	650	620–670	*n* = 2[a]	525	452–591	*n* = 3

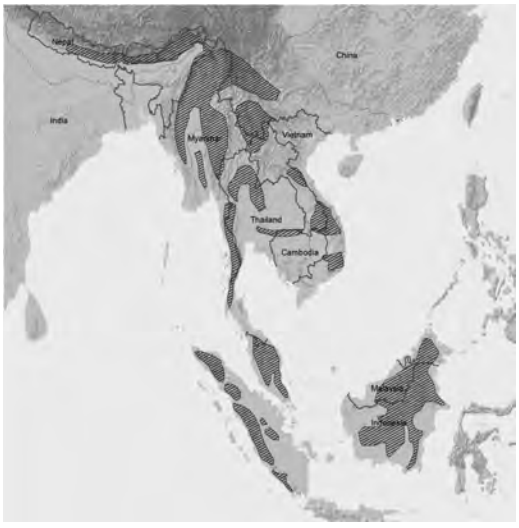
Ref: Kitchener *et al*. (2004)
[a] Sunquist and Sunquist (2002)

cat *P. temminckii*, the two having diverged *c*. 4 million years ago, well before the isolation of Borneo (Johnson *et al*. 1999; O'Brien and Johnson 2007). There are relatively few records for this species, but historically it probably occurred throughout Borneo (Azlan and Sanderson 2007; Meijaard 1997; IUCN 2008). The Borneo bay cat has been reported from hill, lowland, and swamp forest (Meijaard 1997; Azlan *et al*. 2003; Hearn and Bricknell 2003; Azlan and Sanderson 2007; Yasuda *et al*. 2007) and regenerating logged forest (Nowell and Jackson 1996; Hearn and Bricknell 2003; Kitchener *et al*. 2004; Meijaard *et al*. 2005a). Its diet is unknown, and it occurs in both a reddish and grey colour phase (Nowell and Jackson 1996; Sunquist and Sunquist 2002). Observations and camera trap photos have occurred at midday (Azlan *et al*. 2003; Yasuda *et al*. 2007), early morning (Hearn and Bricknell 2003), and at night (Dinets 2003; Meijaard *et al*. 2005a). Outside protected areas, habitat loss due to commercial logging and oil palm plantations is the major threat. Wildlife traders are aware of the species' rarity, and bay cats have been captured illegally from the wild for the skin and pet markets (Sunquist and Sunquist 2002; Kitchener *et al*. 2004; Azlan and Sanderson 2007). The Borneo bay cat is one of the few small cats classified as Endangered on the IUCN Red List of Threatened Species (IUCN 2008).

Map 8 Borneo bay cat. © IUCN Red List 2008.

Marbled cat *Pardofelis marmorata* (Martin, 1837)

The marbled cat resembles a miniature clouded leopard, with a tail equivalent to head–body length and markings so similar that Corbett and Hill (1992) grouped the two species in one genus, on the grounds that 'the unique and complex pattern of the pelage is unlikely to be independently derived or primitive'. Another similar trait is its relatively enlarged upper canines (Groves 1982). However, genetic analysis does not support a close relationship (Johnson *et al*. 2006b; Eizirik *et al*., in prep). The marbled cat is found in tropical Indomalaya (Map 9), along the Himalayan foothills into southwest China, and on the islands of Sumatra and Borneo, and appears to be relatively rare (Nowell and Jackson 1996; Duckworth *et al*. 1999; Holden 2001; Sunquist and Sunquist 2002; Grassman *et al*. 2005a; Azlan *et al*. 2006; Lynam *et al*. 2006; Mishra *et al*. 2006; Yasuda *et al*. 2007), although a higher encounter rate was recorded in Cambodia (13 camera trap records, compared to 12 for the Asiatic golden cat and 4 for the clouded leopard; Duckworth *et al*. 2005). The marbled cat is primarily associated with moist and mixed deciduous–evergreen tropical forest (Nowell and Jackson 1996), and may prefer hill forest (Duckworth *et al*. 1999; Holden 2001; Grassman *et al*.



Map 9 Marbled cat. © IUCN Red List 2008.

2005a)—habitats undergoing the world's fastest deforestation rate (1.2–1.3% a year since 1990; FAO 2007), due to logging, oil palm, and other plantations, and human settlement and agriculture. Grassman and Tewes (2002) reported the observation of a pair of adult marbled cats in a salt lick in Thailand's Phu Khieu National Park, where Grassman *et al.* (2005a) estimated a home range of 5.3 km^2 for an adult female radio-tracked for 1 month. The marbled cat probably preys primarily on rodents, including squirrels (Nowell and Jackson 1996), and birds. Most camera trap records have been diurnal (Duckworth *et al.* 1999; Grassman and Tewes 2002). Although infrequently observed in the illegal Asian wildlife trade (Nowell and Jackson 1996), it is valued for its skin, meat, and bones; indiscriminate snaring is prevalent throughout much of its range (IUCN 2008). They have been reported as poultry pests (Nowell and Jackson 1996; Mishra *et al.* 2006). The marbled cat is classified as Vulnerable (IUCN 2008).

	Male		Female		
		Sample size	Mean	Range	Sample size
Weight (kg)			3.1	2.5–3.7	*n* = 2
Head/body length (mm)	525	*n* = 1	555	490–620	

Ref: Sunquist and Sunquist (2002)

Asiatic golden cat *Pardofelis temminckii* (Vigors and Horsfield, 1827)

The genus *Pardofelis* contains three cats that resemble other species. This species' doppelgänger is the African golden cat, which it resembles in size, appearance, and name. However, genetic analysis has determined that they are not closely related (Johnson *et al.* 2006b; O'Brien and Johnson 2007; Eizirik *et al.*, in prep). The Asiatic golden cat has a similar distribution to the congeneric marbled cat (Map 10). However, it has a larger range in China, like the clouded leopard, and it does not occur on the island of Borneo (Nowell and Jackson 1996; Sunquist and Sunquist 2002). The Asiatic golden cat is primarily found in forest, habitats, ranging from tropical and subtropical evergreen to mixed and dry deciduous forest (Nowell and Jackson 1996), and occasionally in shrub and grasslands (Choudhury 2007). Grassman *et al.* (2005a) found radio-collared golden cats used closed forest and more open habitats in proportion to their occurrence. In Sumatra's Kerinci Seblat National Park, all records for this species were from lowland forest, with none from montane forest, unlike the clouded leopard and marbled cat (Holden 2001). Mishra *et al.* (2006) also found clouded leopard and marbled cat, but no Asiatic golden cat, in the hill forests of India's western Arunachal Pradesh province. However, Wang (2007) obtained camera trap photos of the Asiatic golden cat at an elevation of 3738 m in Bhutan's Jigme Sigye Wangchuk

Map 10 Asiatic golden cat. © ICUN Red List 2008.

Plate F Asiatic golden cat *Pardofelis temminckii*. © Alex Silwa.

National Park in an area of dwarf rhododendron and grassland, an elevation record for the species. Activity readings from two radio-collared golden cats in Thailands's Phu Khieu National Park showed daytime and crepuscular activity peaks (Grassman *et al.* 2005a). Seven of 15 camera trap records in Sumatra's Kerinci Seblat National Park were diurnal (Holden 2001). An adult female Asiatic golden cat in Thailand's Phu Khieu National Park had a home range of 32.6 km^2, overlapped 78% by a male range of 47.7 km^2. Golden cat home ranges were 20% larger than those of clouded leopard, although they were similar in activity and mean daily distance moved (Grassman *et al.* 2005a). One scat contained the remains of Indochinese ground squirrel (Grassman *et al.* 2005a), others from Sumatra contained rat and muntjac remains, and one stomach from Thailand's Kaeng Krachan National Park contained a small snake (Grassman 1998b). It is capable of taking small ungulates (Sunquist and Sunquist 2002). While the reddish-gold pelage the cat is named for is the most common form, there are spotted (Wang 2007) and melanistic morphs (Holden 2001; Grassman *et al.* 2005a). The Asiatic golden cat is Near Threatened due to habitat loss, illegal hunting, and depletion of the wild ungulate prey base (IUCN 2008).

	Male		Female	
		Sample size		Sample size
Weight (kg)	13.5	$n = 1$	7.9	$n = 1$
Head/body length (mm)	910	$n = 1$	770	$n = 1$

Ref: Grassman *et al.* (2005a)

African golden cat *Caracal aurata* (Temminck, 1827)

While the Neotropical and Indomalayan regions have several sympatric forest-dependent felids, the golden cat is Africa's only one (Map 11). The African golden cat occurs mainly in primary moist equatorial forest, although it penetrates savannah areas along riverine forest. It also occurs in montane forest and alpine moorland in the east of its range (Nowell and Jackson 1996; Ray and Butynski, in press). Two studies of scats—from the Ituri forest of the Congo (Hart *et al.* 1996) and the Dzanga-Sangha forest of the Central African Republic (Ray and Sunquist 2001)—found that rodents made up the majority of prey items (frequency of occurrence: 70% and 62%, respectively), followed by small- and medium-sized duiker antelopes (25% and 33%) and primates (5%). Other reported prey items include birds, pangolin (*Manis gigantea*), and in southern Sudan a female with two kittens was observed hunting bats as they swooped over fallen mangoes (Ray and Butynski, in press). African golden cat remains were found in five of 196 leopard *Panthera pardus* scats from Gabon's Lopé National Park (Henschel *et al.* 2005); a single carcass killed by a leopard was found in the Ituri (Hart *et al.* 1996). The African golden cat is Near Threatened by deforestation, prey depletion caused by bushmeat offtake, and by-catch (IUCN 2008). Over 3 months at four sites in Lobeké, south-east Cameroon, 13 African golden cats were snared (T. Davenport, personal communication in Ray *et al.* 2005). Skins are seen in markets, for example in Yaoundé and Kampala, alongside medicinal herbs and fetishes (T. Davenport, personal communication in Ray and Butynski, in press).

Map 11 African golden cat. © IUCN Red List 2008.

Caracal *Caracal caracal* (Schreber, 1776)

The caracal is a long-legged, medium-sized felid, tawny red with large black-backed ears tipped with prominent tufts of hair. It is widely distributed across the drier regions of Africa, central Asia, and south-west Asia into India (Map 12). Its historical range mirrors that of the cheetah, and both coincide with the distribution of several small desert gazelles (Sunquist and Sunquist 2002). Like cheetahs, caracals were captured and trained to hunt by Indian royalty for small game and birds (Divyabhanusinh 1995). Stuart (1982) recorded that between 1931 and 1952 an average of 2219 caracals per year were killed in control operations in the Karoo, South Africa. Similarly, Namibian farmers responding to a government questionnaire reported killing up to 2800 caracals in 1981 (Nowell and Jackson 1996; Stuart and Stuart, in press). Predation on small stock and introduced springbok was seasonal when alternative wild prey was scarce (Avenant and Nel 2002). No livestock were found in 200 caracal scats in the vicinity of South Africa's Mountain Zebra National Park where wild prey was abundant (Grobler 1981). The home

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	11.0	8.0–14.0	*n* = 6	7.2	6.2–8.2	*n* = 2
Head/body length (mm)	766	616–935	*n* = 18	699	630–750	*n* = 8

Source: Ray and Butynski (in press)

Plate G Caracal *Caracal caracal*. © M. G. L. Mills.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	12.9	7.2–19	*n* = 77	10	7–15.9	*n* = 63
Head/body length (mm)	868	750–1080	*n* = 98	819	710–1029	*n* = 94

Ref: Stuart and Stuart (in press)

ranges of three males averaged 316.4 km^2 on Namibian ranch land (Marker and Dickman 2005). In Saudi Arabia, a radio-tracked male ranged over 270 km^2 to 1116 km^2 in different seasons (van Heezik and Seddon 1998), while in an Israeli study, home ranges of five males averaged 220.6 km^2 (Weisbein and Mendelssohn 1989). In the better-watered West Coast National Park of South Africa, two males averaged 26.9 km^2, completely overlapping smaller (7.39 km^2) female ranges (Avenant and Nel 1998). Based on spoor tracking in the Kalahari desert, Melville and Bothma (2007) found a hunting success rate of 10%. The caracal is listed as Least Concern, being widespread and relatively common, particularly in southern and eastern Africa, although there have been range losses in north and west Africa (Ray *et al.* 2005), and is of conservation concern in most of its Asian range (IUCN 2008).

Map 12 Caracal. © IUCN Red List 2008.

Serval *Leptailurus serval* (Schreber, 1776)

Molecular phylogeny reveals that the serval is closely allied with the African golden cat and caracal (Johnson *et al*. 2006b, Eizerik *et al*. in press), diverging from a common ancestor ~5.4 million years ago (O'Brien and Johnson 2007). It is found in the well-watered savannah long-grass habitats of sub-Saharan Africa (Map 13), particularly associated with wetlands and other riparian vegetation, but also in dry forest and alpine grasslands up to 3800 m on Mount Kilimanjaro. In north Africa, they are very scarce in semi-desert and cork oak forest on the Mediterranean coasts of Morocco and possibly Algeria (Cuzin 2003; De Smet 1989, personal communication 2007). Extinct in Tunisia, a population has been re-introduced into Feijda National Park (K. De Smet in Hunter and Bowland, in press). Servals are able to tolerate agriculture provided cover is available (Hunter and Bowland, in press), and may also benefit from forest clearance and the resulting encroachment of savannah at the edges of the equatorial forest belt (Ray *et al*. 2005). With its long legs and large ears, the serval specializes on small mammals, particularly rodents, with 90% of the diet weighing <200 g (Sunquist and Sunquist 2002). Birds are the second most frequent prey item (Hunter and Bowland, in press). Frogs occurred in 77% of scats collected during a study in Tanzania's Ngorongoro crater, and one male ate at least 28 frogs in 3 h (Geertsema 1985). Servals have a characteristic high pounce when hunting, used even for the rare instances of larger prey, which can span 1–4 m and may be up to 2 m high (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Hunter and Bowland, in press). Geertsema (1985) found a hunting success of 49% of almost 2000 pounces, with no significant difference between daylight and moonlit night. Servals killed 15–16 times/24 h, making 0.8 kills per hour during the day and 0.5 kills per hour at night. Juveniles killed more frequently, but hunted smaller prey with lower energy yields. Wetlands harbour comparatively high rodent densities compared with other habitat types, and form the core areas of serval home ranges (Geertsema 1985; Bowland 1990). The home ranges of two females and one male on farmland and an adjacent nature reserve in the KwaZulu-Natal Drakensberg were 19.8 km^2, 15.8 km^2, and 31.5 km^2, respectively (Bowland 1990). In Ngorongoro Crater, Tanzania, the home ranges of an adult female and adult male were 9.5 km^2 and 11.5 km^2, respectively (Geertsema 1985). The minimum density of servals in optimal habitat in Ngorongoro Crater was 42 animals/100 km^2 (Geertsema 1985). The serval is classified as Least Concern, being relatively abundant and widespread (and even expanding). However, degradation of wetlands is of concern, as is the level of skin trade in west Africa (Ray *et al*. 2005; Hunter and Bowland, in press). Servals are rare south of the Sahara in the Sahel region (Clement *et al*. 2007). Servals north of the Sahara are Critically Endangered, with only fewer than 250 mature individuals (IUCN 2008).

Map 13 Serval. © IUCN Red List 2008.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	11.2	9.8–12.4	*n* = 6	8.5	7–9.8	*n* = 7
Head/body length (mm)	853	750–920	*n* = 5	778	725–820	*n* = 5

Source: Bowland (1990)

Pampas cat *Leopardus colocolo* (Molina, 1782)

Named for the Argentine grasslands, the pampas cat is a cat of open habitats, ranging north through the dry forests and scrub grasslands of Bolivia, Paraguay, and Brazil, and up the Andes mountain chain from Chile to Ecuador and possibly marginally into south-western Colombia (Silveira 1995; Nowell and Jackson 1996; Ruiz-García *et al.* 2003; Dotta *et al.* 2007; Map 14). Yet Pereira *et al.* (2002) found few recent records for this species from the Argentine pampas, but more from a semi-arid climatic strip that enters north-western Argentina as a continuation of the Andes and expands south towards the Atlantic coast. In the high Andes, although it has been recorded at over 5000 m (Nowell and Jackson 1996), most records are from lower elevations than the Andean cat *L. jacobita*—in northern Argentina, the mean elevation for pampas cat records was 3567 ± 67 m, as compared to 4236 ± 140 m for the Andean cat (Perovic *et al.* 2003). While in the Andes the pampas cat is easily confused with the Andean cat (rusty-coloured oblong spots on the sides against a grey background), elsewhere the species looks different. In Brazil, it has barely discernible spotting, a shaggier, brownish coat, and black feet (García-Perea 1994; Silveira 1995). A melanistic form exists (Silveira *et al.* 2005). Silveira *et al.* (2005) suggest that the species' similarity to the domestic cat has caused under-recording, as camera traps reveal them to be common in Emas National Park (T. de Oliveira, personal communication 2008). On the basis of morphology, García-Perea (1994) proposed that the pampas cat consists of three species, but genetic analysis does not support this (Johnson *et al.* 1999; Eizirik *et al.*, in prep). Pampas cat prey includes small mammals and ground-dwelling birds (Nowell and Jackson 1996; Silveira *et al.* 2005) and, in the high Andes, mountain viscacha (*Lagidium* spp.) and small rodents (Walker *et al.* 2007; Napolitano *et al.* 2008). In Brazil's Emas National Park, home range size (90% MCP) was estimated at 19.47 ± 3.64 km^2 (Silveira *et al.* 2005). Primarily diurnal with some crepuscular and occasionally nocturnal activity, the pampas cat is listed as Near Threatened due to habitat loss and degradation, as well as retaliatory killing for poultry depredation hunting for traditional cultural purposes in the high Andes (IUCN 2008).

	Male		Female	
	Mean±SD	Sample size	Mean±SD	Sample size
Weight (kg)	3.9 ± 0.6	*n* = 10	4.0	*n* = 2
Head/body length (mm)	682 ± 8	*n* = 10	620 ± 3	*n* = 2

Ref: Silveira *et al*. (2005)

Map 14 Pampas cat. © IUCN Red List 2008.

Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny and Gervais, 1844)

Like the pampas cat, the Geoffroy's cat is found in open habitats and the two are sympatric for much of their range, although Geoffroy's cat does not extend as far north (Map 15). The Geoffroy's cat is distributed throughout the pampas grasslands and dry Chaco shrub and woodlands, and around the alpine saline desert of north-western Argentina to 3300 m in the Andes (Nowell and Jackson 1996). Most of its range is arid or semi-arid (Pereira *et al.* 2006), but it also occurs in wetlands (Sunquist and Sunquist 2002). Lucherini *et al.* (2000) found that forest fragments tended to be used for faecal and scent-marking sites, while grasslands and marshes were used for hunting and resting. In three Argentinian studies cats used dense vegetation (Manfredi *et al.* 2007). Manfredi *et al.* (2004)

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	6.2	4.3–7.8	$n = 4$	4.0	3.5–4.3	$n = 4$
Head/body length (mm)	683	630–740	$n = 4$	628	610–650	$n = 4$

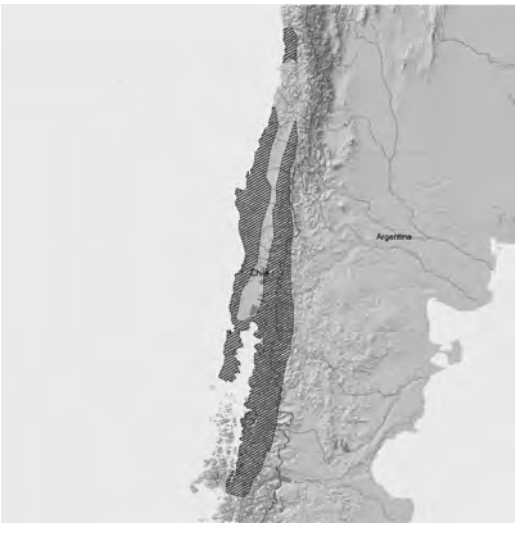
Ref: Lucherini *et al*. (2000)

Map 15 Geoffroy's cat. © IUCN Red List 2008.

found local variation in diet in Argentina, consisting primarily of small rodents, supplemented with birds; small mammals made up 63% of food items in Lihue Calel National Park (Bisceglia *et al.* 2007). In Chile, rodents (including viscachas) and introduced hares were primary prey (Johnson and Franklin 1991; Branch 1995; Pereira *et al.* 2006). Fish and frog remains were found in the stomachs of Geoffroy's cats from Uruguay and Brazil (Sunquist and Sunquist 2002). In wet pampas grassland of Argentina, Manfredi *et al.* (2006) found mean home ranges of 2.5–3.4 km^2, with males' 25% larger than females'. In Chile's Torres del Paine National Park, in *Nothofagus* beech forest, home ranges were larger, at 2.3–6.5 km^2 for two females, and 10.9–12.4 km^2 for two males (Johnson and Franklin 1991). In Lihue Calel National Park, female home ranges averaged 2.5 km^2 during a drought period, in which six radio-collared cats died of starvation, and densities ranged from 2–36/100 km^2 but increased to 139.9 $\pm$ 35.5, 2 years later (Pereira *et al.* 2006; J. Pereira, personal communication 2008). In the Bolivian Chaco, densities ranged from 2–42/100 km^2 (Cuellar *et al.* 2006). An average of 116,000 pelts per year were exported from Argentina alone in the mid-1970s, and 55,000 per year in the early 1980s. However, little trade has taken place after 1988, and the species was upgraded to CITES Appendix I in 1992, prohibiting commercial trade (Nowell and Jackson 1996). Geoffroy's cats are still killed as livestock predators, and these pelts may be traded illegally. It is classified as Near Threatened due to habitat loss and fragmentation (IUCN 2008).

Guiña *Leopardus guigna* (Molina, 1782)

The guiña (kodkod) is the smallest felid in the Americas. It also has the smallest distribution, occurring only in central and southern Chile and marginally in adjoining areas of Argentina (Map 16). Its range is largely coincident with the Valdivian temperate moist forest, recognized as a Global 200 threatened



Map 16 Guiña. © IUCN Red List 2008.

Plate H Guiña *Leopardus guigna*. © Gerardo Acosta-Jammet.

eco-region (WWF 2006), and in the south it is also found in *Nothofagus* beech forest (Freer 2004), which has a high degree of endemism (Armesto *et al.* 1998). Native forest, which is preferred, is being lost to less suitable pine plantations (Acosta-Jamett *et al.* 2003; Acosta-Jamett and Simonetti 2007). Although the guiña is forest-dependent, selecting areas of thicket understory, they use a variety of more open scrub habitat types (Dunstone *et al.* 2002). Over most of its range, the guiña is the only small felid to occur, although it is sympatric in Argentina with its closest relative the Geoffroy's cat (O'Brien and Johnson 2007), which it resembles with its multitude of small black spots, in Argentina (Lucherini *et al.* 2001). Guiñas in southern Chile fed primarily on small mammals, especially rodents, as well as birds, and scavenge opportunistically (Freer 2004). On Chile's Chiloe Island, in a largely agricultural landscape, Sanderson *et al.* (2002c) found home ranges of 6.5 km^2 and 1.2 km^2 for females. Freer (2004) reported smaller home ranges (MCP95) of 1.3 km^2 for males and 1 km^2 for females from two national parks (Laguna San Rafael and Queulat) in southern Chile, where densities were 1 adult-subadult/km^2 (Dunstone *et al.* 2002). Much of their southern range is relatively free of human disturbance (Dunstone *et al.* 2002), but in central Chile there has been substantial habitat loss and there Acosta-Jamett *et al.* (2003) estimated *c.* 2000 individuals in 24 subpopulations. In southern Chile, 81.4% of 43 families considered it 'damaging or very damaging', although there was only a single recent report of a guiña killing 12 hens in a henhouse (Silva-Rodriguez *et al.* 2007), and on Chiloe Island, two out of five radio-collared cats were killed while raiding chicken coops (Sanderson *et al.* 2002c). It is classified as Vulnerable (IUCN 2008).

	Male		Female	
	Mean±SD	Sample size	Mean±SD	Sample size
Weight (kg)	1.8 ± 0.16	*n* = 7	1.4 ± 0.07	*n* = 6
Head/body length (mm)	412 ± 15	*n* = 7	394 ± 7	*n* = 6

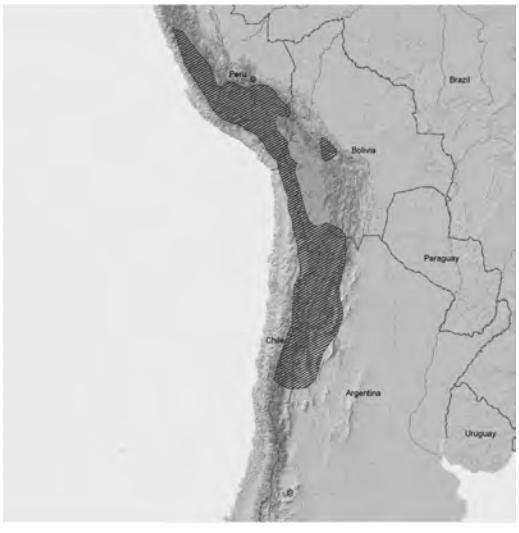
Source: Dunstone *et al.* (2002)

Andean cat *Leopardus jacobita* (Cornalia, 1865)

The Andean cat is restricted to the arid, sparsely vegetated areas of the high Andes in Argentina, Bolivia, Chile, and Peru (Map 17), inhabiting rocky and steep terrain at elevations generally above 4000 m across most of its range (Perovic *et al*. 2003; Cossíos *et al*. 2007b; Napolitano *et al*. 2008; Villalba *et al*., in press; Marino *et al*., Chapter 28, this volume), but as low as 1800 m in the southern Andes (Sorli *et al*. 2006). Its distribution is similar to the historic range of the mountain chinchilla *Chinchilla brevicaudata* (Yensen and Seymour 2000), which was hunted to the brink of extinction for the fur trade a century ago (IUCN 2008), and the diet reveals a preference for another chinchillid, the mountain viscacha (Walker *et al*. 2007; Napolitano *et al*. 2008), which lives in patchily distributed small colonies and has also declined through hunting pressure. The Andean cat is rare compared to its close relative the pampas cat (Lucherini and Vidal 2003; Perovic *et al*. 2003; Cossíos *et al*. 2007b; Napolitano *et al*. 2008; Villalba *et al*., in press), from which it is hard to distinguish in the high Andes (García-Perea 2002; Cossíos *et al*. 2007a; Palacios 2007; Villalba *et al*., in press). Napolitano *et al*. (2008) found reduced genetic diversity in an Andean cat population in northern Chile, suggesting a 'smaller current or historic population size'. Based on genetic sampling in their study area, they estimated a density of one individual per 5 km^2. The Andean cat (as well as the pampas cat) is traditionally considered a sacred animal by indigenous Aymara and Quechua people. Throughout its range, dried and stuffed specimens are kept by local people for use in harvest festivals (Iriarte 1998; Sanderson 1999; Perovic *et al*. 2003; Villalba *et al*. 2004; Cossíos *et al*. 2007b; Villalba *et al*., in press). Hunting for such cultural practices may represent a significant threat. Napolitano *et al*. (2008) found that the probability of finding sign of the Andean mountain cat decreased with proximity to human settlement. The Andean cat is one of the few small felids classified as Endangered (IUCN 2008). There are none known to be kept in captivity, and very few museum specimens.

	Unknown sex	Female
Weight (kg)		4.5[a]
		n = 1
Head/body length (mm)	740–850[b]	
	n = 11	

Sources: [a] Delgado *et al*. (2004); [b] García-Perea (2002), from museum skins of adults' unknown sex



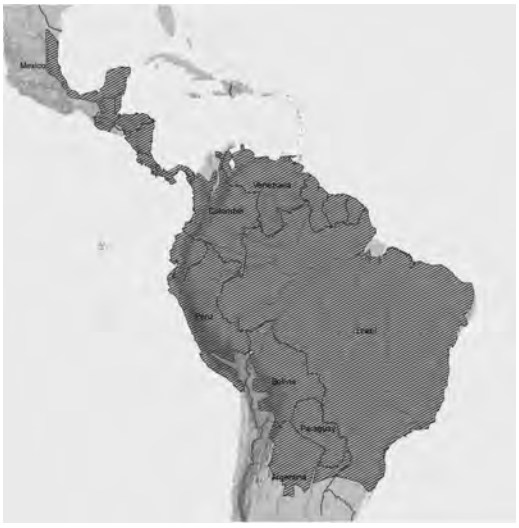
Map 17 Andean cat. © IUCN Red List 2008.

Ocelot *Leopardus pardalis* (Linnaeus, 1758)

The ocelot is the only medium-sized cat found in the neotropics, and one of the most widespread and successful (Map 18). Historically, it ranged as far north as the American states of Arkansas and Arizona, but is now restricted to a small population of 80–120 in southern Texas (Sunquist and Sunquist 2002). In Mexico, it has disappeared from most of its historic range along the western coast, but still occurs on the eastern coast, and south through Central America into South America, where it is found in every country except Chile (IUCN 2008). The ocelot occupies a wide spectrum of habitats, including mangrove forests and coastal marshes, savannah grasslands and pastures, thorn scrub, and tropical forest of all types (primary, secondary, evergreen, seasonal, and montane, although it typically occurs at

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	13.6	12–15.5	*n* = 7	9.8	9–11.3	*n* = 7
Head/body length (mm)	810	770–855	*n* = 7	770	740–795	*n* = 7

Source: Crawshaw (1995)



Map 18 Ocelot. © IUCN Red List 2008.

elevations below 1200 m; Nowell and Jackson 1996). Their prey is mostly terrestrial, nocturnal, and weighs less than 1 kg (Sunquist and Sunquist 2002), although larger prey is also taken. Diet varies with prey availability—in the seasonally flooded savannahs of Venezuela, ocelots fed intensively on land crabs when they became abundant during the wet season (Ludlow and Sunquist 1987). Home ranges vary from 1.8 to 30 km^2 for females and 5.4–38.8 km^2 for males (with much larger home ranges suggested by an ongoing study in the dry savannah of Brazil's Emas National Park). Variation is probably correlated with prey availability, and densities average 32 ± 22/100 km^2, typically much higher than sympatric small felids (Oliveira *et al.*, Chapter 27, this volume). As many as 200,000 animals were hunted yearly for the fur trade in the late 1960s and early 1970s. Concern over the impact of the Neotropical spotted cat skin trade was a major impetus for the establishment in 1975 of CITES, the Convention on International Trade in Endangered Species of Wild Flora and Fauna, which regulates wildlife trade between countries (Nowell and Jackson 1996). Although some illegal skin trade persists, habitat loss is the major threat to the ocelot, although it is classified as Least Concern due to its wide range and abundance in the Amazon (IUCN 2008).

Oncilla *Leopardus tigrinus* (Schreber, 1775)

Although it resembles a smaller version of the ocelot and margay, species formerly considered its closest relatives, genetic analysis groups the oncilla with the guiña and Geoffroy's cat (O'Brien and Johnson 2007). Its distribution is also broadly similar to the ocelot and margay (Map 19), but apparently patchier in the Amazon basin (Oliveira 2004), and with several

Map 19 Oncilla. © IUCN Red List 2008.

Plate I Oncilla *Leopardus tigrinus*. © Projecto Gatos do Mato Brasil.

large gaps—the Llanos grassland of Colombia and Venezuela, the Paraguayan Chaco, and southern Panama (IUCN 2008). Genetic divergence between populations in Costa Rica and southern Brazil is comparable to that between species in the *Leopardus* group, suggesting that the two populations have been isolated for ~3.7 million years. Both groups had relatively low levels of genetic diversity (Johnson *et al.* 1999). While in Central America and parts of northern South America it may be most common in montane cloud forest, it is mostly found in lowland areas in Brazil, being reported from rainforests to dry deciduous forest, savannahs, semi-arid thorny scrub, and degraded secondary vegetation in close proximity to human settlement (Oliveira *et al.* 2008). Although it has been collected as high as 4800 m (Cuervo *et al.* 1986), this is likely an outlier, as there are very few records at or slightly above 3000 m (T. de Oliveira, personal communication). Oncilla are nocturno-crepuscular, but with considerable daytime activity. Diet consists mostly of small mammals, birds, and lizards, with average prey size at <100 g, but does include larger sized prey (>1 kg). Home ranges are larger than predicted from body size (0.9–2.8 km^2 for females and 4.8–17 km^2 for males; Oliveira *et al.*, Chapter 27, this volume). Densities vary from 1/100 km^2 to 5/100 km^2, and in the Amazon may be as low as 0.01/100 km^2 (Oliveira *et al.* 2008). The oncilla is negatively impacted by ocelots, and may not be viable wherever ocelots are present ('ocelot effect'; Oliveira *et al.*, Chapter 27, this volume). With relatively higher densities outside protected areas, the oncilla is threatened by habitat loss and classified as Vulnerable on the IUCN Red List (IUCN 2008).

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	2.6	1.8–3.5	$n = 20$	2.2	1.8–3.2	$n = 15$
Head/body length (mm)	506	430–591	$n = 31$	467	400–514	$n = 27$

Source: Sunquist and Sunquist (2002)

Margay *Leopardus wiedii* (Schinz, 1821)

The margay has broad feet, flexible ankles, and a long tail, all adaptations for arboreality (Nowell and Jackson 1996). In captivity, the margay is well known for its climbing and jumping acrobatics. One young margay 'would start running across a slack clothesline no more than half an inch in diameter, lose his balance, swing under it, then move paw over paw the rest of the way up a slight incline. Coming down, he would hook his paws around the line and slide down head first' (Wiley 1978, in Sunquist and Sunquist 2002). A wild radio-collared margay in Belize was observed feeding and travelling in trees, but also moved between hunting areas on the ground, up to 6 km/day (Konecny 1989). The margay is more forest-dependent than the ocelot and oncilla, reaching greatest abundance in lowland rainforest (Oliveira *et al.* 2008). It also occurs in dry deciduous forest (Nowell and Jackson 1996), but seems to be absent from the semi-arid caatinga scrub of Brazil, with the possible exception of some evergreen forest enclaves (Map 20). It appears to be intolerant of human settlement and altered habitat (IUCN 2008). One young adult male preferred primary to secondary forest, in a home range of 11 km^2 (Konecny 1989), and Crawshaw (1995) reported a male's range of 15.9 km^2 in subtropical forest of Brazil's Iguaçu National Park. Four males in El Cielo Biosphere Reserve, Tamaulipas, Mexico had an average range of 4.03 km^2, and a female 0.96 km^2 (Carvajal *et al.* 2007). Camera trapping suggests generally <5 individuals/100 km^2, with extremes of 20/100 km^2 (Oliveira *et al.* 2008). Predominantly nocturno-crepuscular (Oliveira 1998b), prey include birds, reptiles, fruit, and insects (Sunquist and Sunquist 2002), generally <200 g (Oliveira 1998b; but see Wang 2002). The margay is Near Threatened, primarily by deforestation (IUCN 2008).

Map 20 Margay. © IUCN Red List 2008.

Canada lynx *Lynx canadensis* (Kerr, 1792)

Like the Iberian lynx, the Canada lynx is a lagomorph specialist, with its primary prey the snowshoe hare *Lepus americanus*. However, it is the only felid known to undergo prey-driven cyclic population declines. Documented from over a century of fur trade records, hare populations cycle through declines approximately every decade, and lynx populations follow with a lag of 1–2 years (Bulmer 1974; O'Donoghue *et al.*, Chapter 25, this volume). Lynx densities peak at 17–45/100 km^2, falling to 2/100 km^2(O'Donoghue *et al.* 2007). The cycle is driven by vegetation quality and both hare and lynx numbers, and its amplitude may be influenced by lynx-trapping pressure (Gamarra and Solé 2000). In most of Canada and Alaska (see Map 21 for current distribution), trapping of Canada lynx is managed for the fur trade. Trapping can reduce lynx populations,

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	3.8	3.4–4	*n* = 4		2.6–3	*n* = 2
Head/body length (mm)	393	370–405	*n* = 4	400	390–410	*n* = 3

Source: Sunquist and Sunquist (2002)

Plate J Canada lynx *Lynx canadensis*. © Kim Poole.

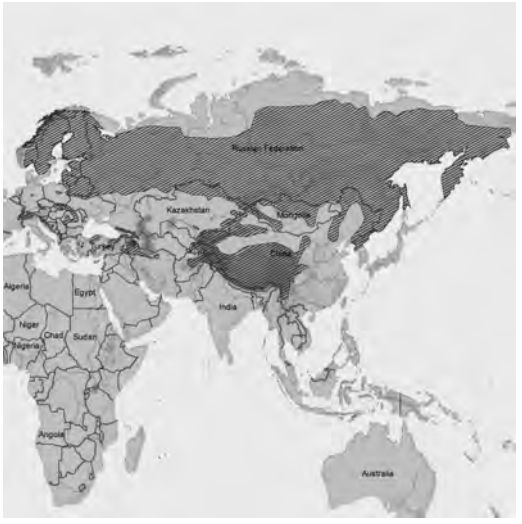
	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	10.7	6.3–17.3	*n* = 93	8.6	5–11.8	*n* = 91
Head/body length (mm)	892	737–1067	*n* = 96	844	762–965	*n* = 89

Ref: Sunquist and Sunquist (2002)

Map 21 Canada lynx. © IUCN Red List 2008.

especially when hare populations cyclically crash. During the cyclic low in the 1980s, most Canadian provinces and Alaska reduced harvests (Mowat *et al.* 2000). From 1980 to 1984, an average of 35,669 Canada lynx pelts were exported from the United States and Canada. That fell between 1986 and 1989 to an average annual export of 7360. Subsequently, annual exports from 2000 to 2006 averaged 15,387 (UNEP-WCMC 2008). Historical information suggests that lynx range and lynx–hare cycles have been largely stable in the north of their range (Mowat *et al.* 2000; Poole 2003). However, in the contiguous United States, lynx formerly occurred in 25 states (McKelvey *et al.* 2000a; Frey 2006), but now just 110,730 km^2 of critical lynx habitat has been proposed for designation in Maine, Minnesota, Washington, and the northern Rocky mountains (USFWS 2008b). A total of 204 lynx from Canada and Alaska have been released successfully since

1999 in the southern Rocky mountains of Colorado, where they are breeding (Nordstrom 2005) and have ranged up to 4310 m, with an average elevation of 3170 m (Wild *et al.* 2006). However, reintroduction of 83 lynx in the late 1980s in northern New York state failed (Sunquist and Sunquist 2002). In eastern Canada where lynx are rare and protected, the primary threat is considered to be interspecific competition from the eastern coyote, which has expanded its range into eastern North America in the past few decades (Parker 2001). In the contiguous United States, the primary threat is habitat fragmentation (Nordstrom 2005). Hybridization with bobcats *Lynx rufus* has been found by genetic analysis in Minnesota (Schwartz *et al.* 2003). The Canada lynx is classified as Least Concern (IUCN 2008).



Map 22 Eurasian lynx. © IUCN Red List 2008.

Eurasian lynx *Lynx lynx* (Linnaeus, 1758)

The Eurasian lynx is the largest lynx, and the only one to take primarily ungulate prey, although they rely on smaller prey where ungulates are scarce (Nowell and Jackson 1996; Breitenmoser *et al.*, Chapter 23, this volume). Lynx kill ungulates ranging in size from the 15 kg musk deer to 220 kg adult male red deer, but show a preference for the smallest ungulate species in the community (Sunquist and Sunquist 2002). Home range averaged 248 km^2 for males ($n = 5$) and 133 km^2 for females ($n = 5$) in Poland's Bialowieza forest (Schmidt *et al.* 1997). Densities are typically one to three adults per 100 km^2, but up to 5/100 km^2 in eastern Europe (Sunquist and Sunquist 2002). The Eurasian lynx occurs from western Europe through the boreal forests of Russia, to central Asia and the Tibetan plateau (Map 22), with much range loss in Europe prior to reintroductions in Switzerland, Slovenia, Czech Republic, Austria, Germany, Italy, and France (Breitenmoser *et al.* 2000; IUCN 2008). The European lynx population (excluding Russia) is estimated at 8000. Populations in central and southern Europe are small and fragmented, although there are larger populations in Fennoscandia and the Baltic states (Breitenmoser *et al.* 2000), and a stronghold in southern Siberian woodland stretching through eastern Russia from the Ural mountains to the Pacific (IUCN 2008); the Russian population has been estimated at 30,000–35,000 (Matyushkin and Vaisfeld 2003). Its status in China is poorly known (IUCN 2008). In Mongolia, Matyushin and Vaisfeld (2003) estimate the lynx population at 10,000. While China and Russia exported nearly 20,000 skins annually in the late 1980s (Nowell and Jackson 1996), this trade has ended (UNEP-WCMC 2008). However, illegal skin trade remains the leading threat to the species, together with habitat loss and prey base depletion (Government of USA 2007a). It is classified as Least Concern (IUCN 2008).

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	19.6	16.3–23.5	$n = 10$	17.3	14–21.5	$n = 12$
Head/body length (mm)	1000	760–1080	$n = 16$	900	850–1000	$n = 21$

Source: Heptner and Sludskii (1992)

Iberian lynx *Lynx pardinus* (Temminck, 1827)

The Iberian lynx is highly specialized on the European rabbit *Oryctolagus cuniculus*. It occurs only west of the Pyrenees on the Iberian Peninsula (Map 23), and its prey base has declined sharply due to habitat loss and disease (Ferreras *et al.*, Chapter 24, this volume). The Iberian lynx is the only cat species listed as Critically Endangered on the IUCN Red List (IUCN 2008). It occurs only in small isolated pockets in arid scrubland of southwestern Spain, but has not been detected in Portugal since the early 1990s, despite intensive surveys (Serra and Sarmento 2006). Surveys in Spain suggest between 84 and 143 adults surviving in two isolated breeding populations (in the Coto Doñana and near Andújar-Cardeña in the eastern Sierra Morena). The Doñana population numbers 24–33 adults and the Sierra Morena is the stronghold of the species, with an estimated 60–110 adults. None of the remaining potential populations in East Montes de Toledo, West Sistema Central, and some areas of central and western Sierra Morena is thought to include animals that breed regularly (IUCN 2008). The latest population estimates indicate a decline of more than 80% from the 880–1150 lynx estimated by surveys in 1987–1988. A similar decline of 80% was estimated for the period 1960–78 (Rodriguez and Delibes 1992). Current numbers are not viable (Delibes *et al.* 2000; IUCN 2008). In the Coto Doñana, total annual home ranges average 9.5 km^2 for adult females and 18.2 km^2 for adult males, with seasonal average adult density of 77/100 km^2 (Palomares *et al.* 2001). Previously considered conspecific with *L. lynx* by some authorities, the Iberian lynx is now accepted as a distinct species on the basis of both genetics (Johnson *et al.* 2006b; Eizirik *et al.*, in prep) and morphology (Werdelin 1981; Wozencraft 2005). The two species are estimated to have diverged ~1 million years ago (O'Brien and Johnson 2007), and were sympatric in central Europe during the late Pleistocene, but in modern times have not co-occurred (Nowell and Jackson 1996).

Map 23 Iberian lynx. © IUCN Red List 2008.

Bobcat *Lynx rufus* (Schreber, 1777)

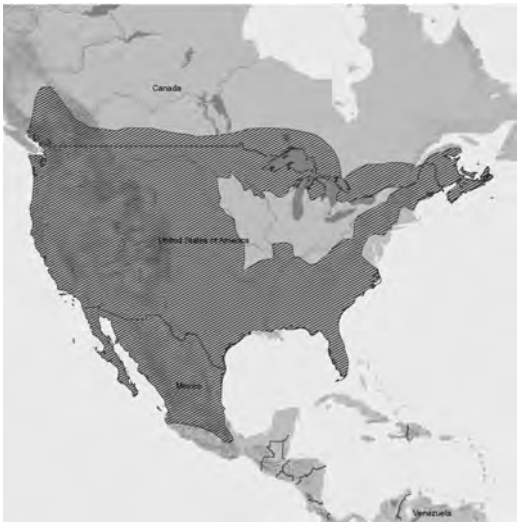
Like its close relative *L. canadensis* the bobcat preys primarily on lagomorphs, but is less of a specialist. Rodents are commonly taken, and bobcats are capable of taking deer weighing up to 10 times their own body weight (Sunquist and Sunquist 2002). Bobcats occur mostly in the United States, but also into central Mexico and southern Canada (Map 24), where their range has been expanding northwards with forest clearance (Nowell and Jackson 1996; Sunquist and Sunquist 2002). While generally favouring low- and mid-elevations, in the western United States they have been trapped at elevations up to 2575 m (Nowell and Jackson

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	12.8	11.1–15.9	*n* = 6	9.3	8.7–9.9	*n* = 4
Head/body length (mm)	787	747–820	*n* = 6	720	782–754	*n* = 6

Ref: Beltrán and Delibes (1993)

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	9.3	5.6–11.4	*n* = 21	6.2	4.2–10.5	*n* = 26
Head/body length (mm)	735	603–927	*n* = 21	624	508–724	*n* = 26

Source: Young (1978)



Map 24 Bobcat. © IUCN Red List 2008.

1996) and in western Mexico, radio-collared bobcats were located at 3500 m on the Colima Volcano (Burton *et al.* 2003). Bobcats are found in both forested and open habitats, which typically include areas with abundant rabbit and rodent populations, dense cover, and shelters that function as escape cover or den sites (Sunquist and Sunquist 2002). In Mexico, bobcats are found in dry scrub and grassland, as well as tropical dry forest including pine, oak, and fir (Monroy-Vilchis and Velazquez 2003; Arzate *et al.* 2007; C. Lopez-Gonzalez, personal communication 2007). Home ranges vary from 6 km^2 for females in southern California to 325 km^2 for male bobcats in upstate New York. Bobcats in northern and western portions of the United States are consistently larger than those in the south, possibly because the warmer climates provide a less variable prey base (Sunquist and Sunquist 2002). Density estimates include 48/100 km^2 in Texas (Heilbrun *et al.* 2006); 25/100 km^2 in Arizona (Lawhead 1984); <9/100 km^2 in Idaho (Knick 1990); and 11/100 km^2 in Virginia (minimal estimate; M. Kelly, personal communication 2007). Bobcat densities in the northern parts of their range are generally lower than in the south (Sunquist and Sunquist 2002). However, the first density estimate for bobcats in Mexico is low, at five individuals per 100 km^2 (Arzate *et al.* 2007). Habitat loss is viewed as the primary threat to bobcats in all three range countries (IUCN 2008). The bobcat is now the leading felid in the skin trade, with most exports coming from the United States. From 1990 to 1999, annual exports averaged 13,494; in 2000–06 the average climbed to 29,772, with a peak of 51,419 skins exported in 2006 (UNEP-WCMC 2008). The US government has repeatedly petitioned the CITES to delist the bobcat from Appendix II to Appendix III (Government of USA 2007b), but has been rejected by majority vote due to concerns about opening a loophole for illegal trade in other felids, all of which are listed on CITES Appendices I or II (Nowell *et al.* 2007). It is classified as Least Concern on the IUCN Red List (IUCN 2008).

Cheetah *Acinonyx jubatus* (Schreber, 1775)

Most famous for its speed (29 m/s; Sharp 1997), the cheetah has a number of adaptations, both morphological (Kitchener *et al.*, Chapter 3, this volume) and behavioural (Durant *et al.*, Chapter 16, this volume) that are unique among felids, and are specializations for catching fleet-footed antelope prey. In areas where large-scale ungulate migration patterns are still intact, such as the Serengeti plains of Tanzania (see map 25), wide-ranging solitary female cheetahs (average home range size: 800 km^2) pass through small temporary territories held by male coalitions (average

Map 25 Cheetah. © IUCN Red List 2008.

territory size: 50 km^2; Caro 1994). However, in areas where prey is non-migratory, male and females have overlapping ranges that are similar in size (Sunquist and Sunquist 2002). On Namibian farmlands, both cheetah sexes have very large home ranges (average 1642 km^2); however, intensively used core areas were just 14% of the total home range (Marker *et al.*, Chapter 15, this volume). Cheetahs are primarily active during the day, perhaps reducing competition (Caro 1994). Other large carnivores, especially lions and hyenas, steal cheetah kills and kill cheetahs. Cheetahs occur at lower densities than would be expected considering their energy needs (Anonymous 2007). On the Serengeti plains, cheetah densities range from 0.8/100 km^{2}to 1.0/100 km^2, but seasonally cheetahs can congregate at densities up to 40/100 km^2 (Caro 1994). Caro (1994) attributes lower cheetah densities to interspecific competition, but on Namibian farmlands, where lions and hyenas have been eradicated, cheetahs still occur at low densities (0.2/100 km^2), despite an abundant wild prey base (Marker *et al.*, Chapter 15, this volume). Namibia is believed to have the largest national cheetah population (2000; Purchase *et al.* 2007), despite decades of extensive trapping by farmers, with over 9500 cheetahs removed from 1978 to 1995 (Nowell 1996). Elsewhere in Africa, cheetahs have lost 76% of their historic range (Ray *et al.* 2005), and disappeared everywhere from their formerly extensive Asian range except for a small population in Iran (60–100 individuals, Hunter *et al.* 2007b; see Map 25 for current range). Cheetahs were captured and trained for hunting by Asian royalty, ranging from the Caucasus to India, for thousands of years (Divyabhanusinh 1995; Sunquist and Sunquist 2002). The species formerly had an even wider range, having originated in North America (with its closest living relatives, the puma and jaguarundi; Johnson *et al.* 2006b). The cheetah exhibits remarkably low levels of genetic diversity in comparison to other felids (O'Brien *et al.* 1985b) (but not compared to carnivores in general; Merola 1994; see Culver *et al.* Chapter 4, this volume). While causes of past low population sizes are unclear, the causes for the cheetah's current state of threat are well known: habitat loss and fragmentation, conflict with people, and depletion of their wild prey base (Marker 2002; Dickman *et al.* 2006a). Interspecific competition with larger predators leads to cheetahs achieving higher densities outside protected areas (Marker 2002). A recent analysis found that known resident cheetah populations in 'classic' cheetah habitat in eastern Africa only occur over approximately 350,000 km^2, with an estimated population of ~2500 (Anonymous 2007). The cheetah is classified as Vulnerable, and Critically Endangered in Iran and North Africa (IUCN 2008).

	Male		Female	
	Mean ± SD	Sample size	Mean ± SD	Sample size
Weight (kg)	41.4 ± 5.4	*n* = 23	35.9 ± 5.3	*n* = 19
Head/body length (mm)	1225 ± 7	*n* = 24	1245 ± 7.5	*n* = 16

Ref: Caro (1994)

Puma *Puma concolor* (Linnaeus, 1771)

Occurring from the mountains of British Columbia to Tierra del Fuego, the puma has the largest geographic range of the New World cats (Map 26); apparently larger than any terrestrial mammal in the western hemisphere (Sunquist and Sunquist 2002). However, it was extirpated over 100 years ago from the eastern half of its historic range in the United States and Canada. Numerous scattered sightings in

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	58.9	56.2–64.4	*n* = 10	30.7	27.2–36.3	*n* = 11
Head/body length (mm)	1347	1260–1440	*n* = 10	1179	1110–1260	*n* = 11

Source: Sweanor (1990)

Map 26 Puma. © IUCN Red List 2008.

the Midwest suggest they may be recolonizing (Anonymous 2005b). DNA analysis of hair samples collected in Fundy National Park, New Brunswick, Canada identified two individual cougars (as they are known in eastern North America), one of North American and one of South American ancestries (Bertrand 2006). This and other evidence suggests that some of the hundreds of reported observations of cougars in eastern North America are escaped captive animals. The only area where panthers (as pumas are known in the south-eastern United States) are known to have survived historical extirpation is a single population in the Everglades swamp forest region of Florida, although it experienced a severe bottleneck (Culver *et al.* 2008), and currently numbers only about 100 (Onorato *et al.*, Chapter 21, this volume). Culver *et al.* (2000) suggest that the lack of genetic variation among North American pumas in general is the result of a late Pleistocene extinction event (as befell the North American cheetah), and later recolonization from the south. Pumas are found in a broad range of habitats, in all forest types as well as lowland and montane desert. Pumas are sympatric with jaguars in much of their Latin American range, and may favour more open habitats than their larger competitor (Vynne *et al.* 2007), although both can be found in dense forest (Sunquist and Sunquist 2002). Pumas are capable of taking large prey, but when available, small- to medium-sized prey are more important in their diet (in tropical portions of the range). This is true of wild prey as well as livestock (IUCN 2008). In North America, deer make up 60–80% of the puma's diet, and the mean weight of prey taken is 39–48 kg. In Florida, however, where deer numbers are low, pumas take smaller prey including feral pigs, raccoons, and armadillos, and deer account for only about one-third of the diet (Sunquist and Sunquist 2002). Bonacic *et al.* (2007) found hares to be the predominant prey (96%) in analysis of scats from the Mediterranean shrub ecoregion of Chile. Densities exceeding four adults per 100 km^2 do not appear to be common in North America (Sunquist and Sunquist 2002). In Chilean Patagonia, density was estimated at 6/100 km^2 (Franklin *et al.* 1999). Kelly *et al.* (2008) reported densities in three study sites as follows: Belize, 2–5/100 km^2; Argentina, 0.5–0.8/100 km^2; and Bolivia, 5–8/100 km^2. Although classified as Least Concern, pumas are threatened by habitat loss and fragmentation, poaching of their wild prey base, and persecution due to livestock depredation (IUCN 2008).

Jaguarundi *Puma yagouaroundi* (Lacépède, 1809)

With its elongated and low-slung body, the jaguarundi has been a taxonomic enigma (Sunquist and Sunquist 2002), but genetic analysis groups it with

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	5.7	5–6.5	$n = 4$	4.1	3.7–4.4	$n = 3$
Head/body length (mm)	693	650–755	$n = 4$	596	550–635	$n = 3$

Ref: A. Caso (personal Communication) in Sunquist and Sunquist (2002)

Map 27 Jaguarundi. © IUCN Red List 2008.

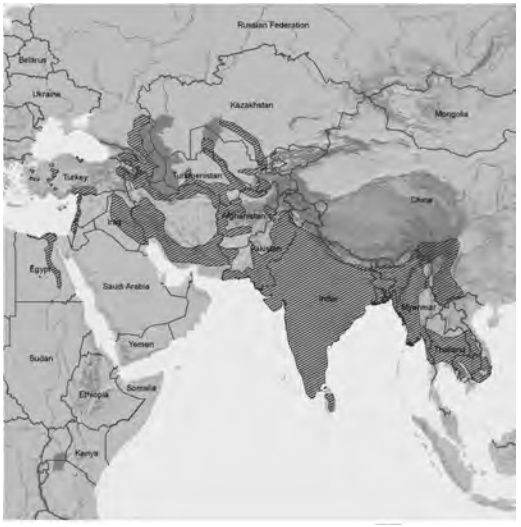
the puma and the cheetah (Johnson *et al.* 2006b; O'Brien and Johnson 2007; Eizirik *et al.*, in prep). Probably extinct in the United States, it ranges from Mexico through Central America and the Amazon basin to central Argentina and Uruguay (IUCN 2008; Map 27). It occurs in a variety of habitats, from closed primary rainforest to open desert, scrub, and grassland, although in open areas it sticks to patches of dense cover (Nowell and Jackson 1996; Oliveira 1998a). Caso and Tewes (2007) found that radio-collared jaguarundis used mature forest 53% of the time and pasture-grassland 47% of the time. It is predominantly a lowland species ranging up to 2000 m, although it was reported up to 3200 m in Colombia (Cuervo *et al.* 1986). It is also predominantly diurnal (with activity peaks in late morning and late afternoon: Caso and Tewes 2007). Jaguarundis occur at relatively low densities of 1–5/100 km^2 in Brazil (Oliveira *et al.* 2008), but reach densities up to 20/100 km^2 in Tamaulipas, Mexico (A. Caso, personal communication 2007). Radio-collared jaguarundis in rainforest of Belize's Cockscomb Basin reserve had much larger home ranges than the sympatric jaguar. One female used a home range that varied between 13 and 20 km^2, while two males used home ranges of 100 and 88 km^2 (Konecny 1989). Home ranges in scrub land of Tamaulipas, Mexico, were smaller, averaging 9.6 km^2 for males and 8.9 km^2 for females. With 20 radio-collared animals in the study area, extensive inter- and intrasexual overlapping of home ranges was documented (Caso and Tewes 2007). Although with its wide range the species is classified as Least Concern, habitat loss is a threat, especially for the more open types, which are being converted to large-scale agriculture (IUCN 2008).

Jungle cat *Felis chaus* (Schreber, 1777)

The jungle cat, despite its name, is not strongly associated with the classic rainforest 'jungle' habitat, but rather with wetlands—habitats with water and dense vegetative cover, especially reed swamps, marsh, and littoral and riparian environments. Hence its other common and more applicable names, the swamp or reed cat. Its preferred microhabitat of water and dense ground cover can be found in a variety of habitat types, ranging from desert (where the cat occurs near oases or along riverbeds) to grassland, shrubby woodland, and dry deciduous forest, as well as cleared areas in moist forest (Nowell and Jackson 1996)—and thus the jungle cat has a broad but patchy distribution from Egypt's Nile River Valley through Asia to the Isthmus of Kra (Map 28). Small mammals, principally rodents, are the primary prey of the jungle cat. A study in India's Sariska reserve estimated that jungle cats catch and eat three to five rodents per day (Mukherjee *et al.* 2004). Birds rank second in importance, but in southern Russia waterfowl are the mainstay of

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	8.1	5–12	*n* = 11	5.1	2.6–7.5	*n* = 14
Head/body length (mm)	763	650–940	*n* = 13	658	560–850	*n* = 13

Ref: Sunquist and Sunquist (2002)



Map 28 Jungle cat. © IUCN Red List 2008.

jungle cat diet in the winter. In India, they have been seen to scavenge kills of large predators such as the Asiatic lion. In a study in southern Uzbekistan, the fruits of the Russian olive made up 17% of their diet in winter. While jungle cats specialize on small prey, they are large and powerful enough to kill young swine, subadult gazelles, and chital fawns (Sunquist and Sunquist 2002). Jungle cats can do well in cultivated landscapes (especially those that lead to increased numbers of rodents) and artificial wetlands. However, as population density in natural wetlands appears to be higher, ongoing destruction of natural wetlands, throughout its range but particularly in the more arid parts, still poses a threat to the species (Nowell and Jackson 1996). Unselective trapping, snaring, and poisoning around agricultural and settled areas have caused population declines in many areas throughout its range (Abu-Baker *et al.* 2003; Duckworth *et al.* 2005). The jungle cat is classified as Least Concern by IUCN (2008), as the species is widespread, and common in some parts of its range, particularly India (Mukherjee 1989). However, population declines and range contraction are of concern elsewhere, particularly Egypt (Glas, in press) and south-west Asia (Abu-Baker *et al.* 2003), the Caucasus (IUCN 2008), central Asia (Habibi 2004), and south-east Asia (Duckworth *et al.* 2005).

Sand cat *Felis margarita* (Loche, 1858)

The sand cat is large-eared, pale in colouration, and the only felid to occur exclusively in desert. The undersides of the feet are thickly furred, which may help it to move across shifting sands and protect the feet from high temperature sand (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Sliwa, in press-a). The claws do not fully retract and are rather blunt—possibly due to the sand cat's digging behaviour (Sunquist and Sunquist 2002; Sliwa, in press-a). It is highly fossorial, known to Saharan nomads as 'the cat that digs holes' (Dragesco-Joffe 1993). During 9 months of radio-tracking four sand cats, on only a single occasion was a study animal observed in daytime outside its burrow, and then only 2 m away (Abbadi 1993). Sand cats use and enlarge burrows of other species as well as digging their own (Sliwa, in press-a). They cover their scats with sand, making diet study difficult. The only scats found by Abbadi (1993) during his study, 'despite painstaking searches on foot the day after our night watches', were inside the box traps that captured the cats. They contained the remains of Cairo spiny mouse (*Acomys cahirinus*) and gecko (*Stenodactylus* spp.). Sand-dwelling rodents made up the majority (65–88%) of stomach contents from carcasses collected in Turkmenistan and Uzbekistan in the 1960s (Schauenberg 1974). Sand cats have also been observed hunting birds and reptiles (Abbadi 1993; Dragesco-Joffe 1993), and will drink water

Plate K Sand cat *Felis margarita*. © Jameson Weston, Hogle Zoo.

readily but can survive on metabolic water (Sliwa, in press-a). They move long distances in a single night (5–10 km; Abbadi 1993). Annual ranges from Saudi Arabia are up to 40 km^2 (M. Strauss, personal communication 2008). The sand cat has a wide but apparently disjunct distribution through the deserts of northern Africa and south-west and central Asia (Hemmer *et al.* 1976; Nowell and Jackson 1996; see Map 29). Sightings have been reported in Libya and Egypt west of the Nile (Sliwa in press-a), but there are no historical records despite intensive collecting effort (Hemmer *et al.* 1976). It is classified as Near Threatened (IUCN 2008) because vulnerable arid ecosystems are being rapidly degraded by human settlement and activity, especially livestock grazing. The sand cat's small mammal prey base depends on adequate vegetation, and may

Map 29 Sand cat. © IUCN Red List 2008.

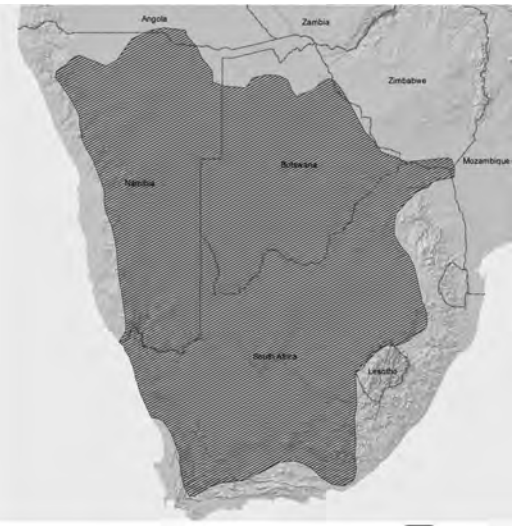
	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	2.78	2.0–3.2	*n* = 4	2.2	1.35–3.1	*n* = 5
Head/body length (mm)	499	460–570	*n* = 5	467	400–520	*n* = 6

Ref: Sunquist and Sunquist (2002)

experience large fluctuations due to drought (Sunquist and Sunquist 2002), or declines due to desertification and loss of natural vegetation.

Black-footed cat *Felis nigripes* (Burchell, 1825)

The black-footed cat, Africa's smallest felid, is endemic to the short grasslands of southern Africa (Map 30), where it is rare and classified as Vulnerable (IUCN 2008). Knowledge of its behaviour and ecology stems from a decade-long study on the Benfontein Game Farm in central South Africa, where more than 20 cats were radio-collared and habituated (Sliwa 2004; Sliwa 2007; Sliwa *et al.*, Chapter 26, this volume). Black-footed cats are solitary, except for females with dependent kittens, and during mating. Males have larger annual home ranges (20.7 km^2, $n = 5$) than females (10.0 km^2, $n = 7$). Male ranges overlap those of 1–4 females. Intra-sexual overlap varies from 12.9% for three males to 40.4% for five females (Sliwa 2004). In his 60 km^2 study area, Sliwa (2004) found the density of adult cats to be 0.17/km^2. Kittens are independent after 3–4



Map 30 Black-footed cat. © IUCN Red List 2008.

Plate L Black-footed cat *Felis nigripes*. © Alex Silwa.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	1.93	1.75–2.45	*n* = 8	1.3	1.1–1.65	*n* = 10
Head/body length (mm)	453	430–520	*n* = 8	397	370–420	*n* = 10

Ref: Sliwa (in press-b)

months, but remain within the range of their mother for extended periods (Sliwa, in press-b). Sliwa (2006) observed 1725 prey items consumed by black-footed cats, with an average size of 24.1 g. Males fed on significantly larger prey (27.9 g) than did females (20.8 g). Mammals were the most common prey item (72%), followed by small birds weighing less than 40 g (26%), while invertebrates, amphibians, and reptiles were infrequently taken. Small rodents like the large-eared mouse *Malacothrix typica*, captured 595 times by both sexes, were particularly important during the reproductive season for females with kittens. Male black-footed cats showed less variation between prey-size classes consumed among climatic seasons. This sex-specific difference in prey size consumption may help to reduce intraspecific competition (Sliwa 2006). The black-footed cat is threatened primarily by habitat degradation by grazing and agriculture, as well as by poison and other indiscriminate methods of pest control (Nowell and Jackson 1996; Sliwa, in press-b).

Wildcat *Felis silvestris* (Schreber, 1777)

The wildcat has the widest distribution of any felid (Map 31), being found throughout the drier regions of Africa into Europe (including Scotland), southwest and central Asia, and Russia (Nowell and Jackson 1996). The house cat was domesticated from the wildcat. Archaeological evidence dates back to the origin of agriculture in the Eastern Crescent, and domestication is presumed to have started with a commensal relationship, with wildcats coming into villages to prey on rodents attracted to grain stores (Clutton-Brock 1999; Driscoll *et al*. 2007). Genetic analysis (Driscoll *et al*. 2007; Eizirik *et al*., in prep) supports five wild subspecies plus a sixth, the domestic cat *F. catus*, which is mitochondrially monophyletic with *F.s. lybica* Forster, 1780 (North Africa and south-west Asia) (Driscoll *et al*. 2007). The taxanomic nomenclature of the domestic cat is complex and controversial and fully discussed in Macdonald *et al*. (Chapter 22, this volume). Other wild sub-species are *F.s. cafra* Desmarest, 1822 (sub-Saharan Africa);

Map 31 Wildcat. © IUCN Red List 2008.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	4.9	4–6.2	*n* = 10	3.7	2.4–5.0	*n* = 10
Head/body length (mm)	601	545–665	*n* = 21	550	460–620	*n* = 15

Ref: Stuart *et al*. (in press)

F.s. ornata Gray, 1830 (central Asia to India); *F.s. bieti* Milne-Edwards, 1872 (western China); and *F.s. silvestris* Schreber, 1775 (Europe). *F.s. bieti* has been previously considered a separate species *F. bieti* (Wozencraft 2005), and has an apparently restricted distribution on the eastern edge of the Tibetan plateau at elevations from 2500 to 5000 m (He *et al.* 2004). Female home ranges vary widely with habitat, from 52.7 km^2 in the United Arab Emirates (Phelan and Sliwa 2005) to 1–2 km^2 in France and Scotland (Stahl *et al.* 1988; Macdonald *et al.*, Chapter 22, this volume). The world's population of domestic cats was estimated at 400 million (Legay 1986), and interbreeding is the main threat to the wildcat (Macdonald *et al.* 2004b; IUCN 2008). Of the subspecies, only *F.s. bieti* shows no evidence of genetic introgression (Driscoll *et al.* 2007).

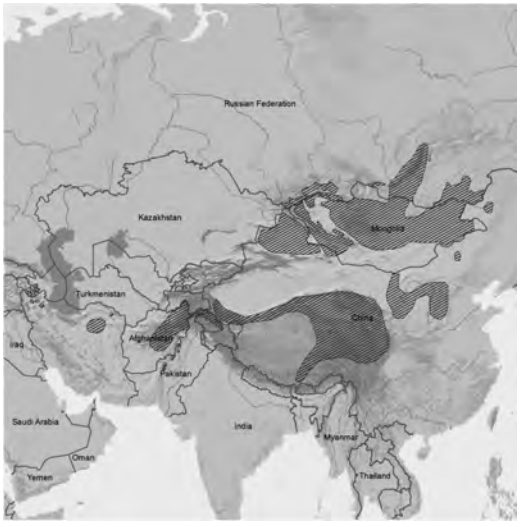
Pallas's cat *Otocolobus manul* (Pallas, 1776)

The cat first described by German explorer Peter Pallas was hardly a typical feline, with its short legs, shaggy fur, and its small rounded head and ears. In Mongolia, it is sometimes mistakenly killed by marmot hunters targeting one of the Pallas's cat's main prey species (IUCN 2008). While it is grouped in the tribe Felini with *Felis* and *Prionailurus*, the exact phylogenetic relationships are unclear and it is retained in the monospecific genus *Otocolobus* by Eizirk *et al.* (in press). Pallas's cat is also known by its Russian name, manul, in Mongolia, Russia, and the former Russian republics of central Asia, which make up the majority of its range (Map 32). It was recently recorded from north-west Iran (Aghili *et al.* 2008), although its current distribution in the trans-Caspian area is poorly known. It also occurs sparsely throughout the Tibetan Plateau, where an elevational record of 5050 m was reported recently (Fox and Dorji 2007). Populations in the south-west of its range (the Caspian Sea region, and Afghanistan and Pakistan) are diminishing, isolated, and sparse (Belousova 1993; Nowell and Jackson 1996; Habibi 2004). Typical habitat for the Pallas's cat is characterized by an extreme continental climate—little rainfall, low humidity, and a wide range of temperatures. They are rarely found in areas where the maximum mean 10-day snow cover depth exceeds 10 cm, and a continuous snow cover of 15–20 cm marks the ecological limit for this species (Sunquist and Sunquist 2002).

Plate M Pallas's cat *Otocolobus manul*. © East Azerbaijan Department of Environment of Iran Public Office.

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	4.12	3.3–5.3	$n = 25$	4.02	3.05–5	$n = 16$
Head/body length (mm)		553 ± 17	$n = 4$	492 ± 20		$n = 10$

Ref: S. Ross (personal communication)

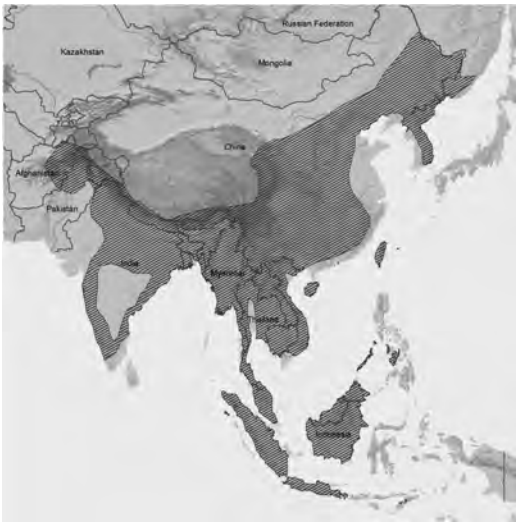


Map 32 Pallas's cat. © IUCN Red List 2008.

In the grass and shrub steppe of central Mongolia, annual home ranges were found to be strikingly large for a small felid, although it is not clear if such large ranges are typical for the species (Brown *et al.* 2003). Ongoing research there (S. Ross, personal communiction 2008) measured mean annual home ranges (95% MCP) at 27.1 ± 23.6 km^2 for adult females (n = 10) and 100.4 ± 101.2 km^2 for males (n = 8). Pallas's cats have a strong association with rocky, steep areas and were rarely found in open grasslands (where they may be more vulnerable to predation by sympatric carnivores; S. Ross, personal communication 2008). In China, Pallas's cats appear to be most numerous where pikas and voles are abundant and not living under deep snow cover (C. Wozencraft, personal communication). In Mongolia, preliminary analysis of scats indicated that gerbils (*Meriones* spp.) and jerboas (*Dipus sagitta* and *Allactaga* spp.) were the main prey, with lambs of the Argali sheep (*Ovis ammon*) taken during the spring (Murdoch *et al.* 2006). Body weight varies widely by season (lowest in winter) and phase in reproductive cycle (lowest for males when breeding and for females after raising kittens). Activity is predominantly crepuscular, although they can be active at any time (S. Ross, personal communication 2008). It is classified as Near Threatened due to prey-base depletion (poisoning and over-hunting), habitat degradation by livestock and agriculture, and illegal trade in skins and for traditional medicine (IUCN 2008).

Leopard cat *Prionailurus bengalensis* (Kerr, 1792)

The leopard cat is common and widespread throughout most of India west into Pakistan and Afghanistan, across most of China, and north to the Korean peninsula, and into the Russian Far East (Map 33). It also



Map 33 Leopard cat. © IUCN Red List 2008.

occurs throughout south-east Asia, and on the islands of Sumatra, Java, Borneo, and Taiwan. The leopard cat is the only wild felid found in Japan, where it occurs on the small islands of Tsushima and Iriomote, and the Philippines, where it occurs on the islands of Palawan, Panay, Negros, and Cebu (IUCN 2008). An excellent swimmer, it is found on numerous small offshore islands of mainland Asia (Nowell and Jackson 1996; Sunquist and Sunquist 2002). Ranging up to 3000 m in the Himalayas, it occurs in habitats from tropical rainforest to temperate broadleaf and, marginally, coniferous forest, as well as shrub forest and successional grasslands. While the leopard cat is more tolerant of disturbed areas than other small Asian felids (Nowell and Jackson 1996; Sunquist and Sunquist 2002), it likely experiences higher mortality in such areas. Higher survival rates (92%) were recorded in a protected area with little human influence, compared with lower rates in areas with greater human activity (53–82%; Haines *et al.* 2004). Based on a large sample size of 20 radio-collared cats in Thailand's Phu Khieu Wildlife Sanctuary, mean home range size (95% MCP) was 12.7 km^2, larger than in other areas of Thailand (4.5 km^2; Grassman *et al.* 2005a), on Borneo (3.5 km^2; Rajaratnam *et al.* 2007), or on Japan's Iriomote island (Schmidt *et al.* 2003). There was no significant difference between male and female home range size. Open and closed forest habitats were used in proportion to their occurrence, and activity patterns showed crepuscular and nocturnal peaks. On Borneo, Rajaratnam *et al.* (2007) found that leopard cats hunted rodents in oil palm plantations, and used forest fragments for resting and breeding. Murids dominate the diet (85–90%; Grassman *et al.* 2005a; Rajaratnam *et al.* 2007). In China, commercial exploitation for the fur trade has been heavy, with annual harvests estimated at 400,000 in the mid-1980s (Nowell and Jackson 1996). Although commercial trade is much reduced, the species continues to be hunted throughout most of its range for fur and food, and captured for the pet trade. They are also widely viewed and persecuted as poultry pests. Leopard cats can hybridize with domestic cats, resulting in the popular domestic breed, the 'safari cat'. Hybridization in the wild has been reported, but is not considered a significant threat. It is classified as Least Concern on the IUCN Red List, but the Iriomote subspecies (Japan) is Critically Endangered, with a population of less than 100, and the West Visayan (the Philippines) leopard cat is Vulnerable due to habitat loss (IUCN 2008).

	Male		Female	
	Mean ± SD	Sample size	Mean ± SD	Sample size
Weight (kg)	2.9 ± 0.38	*n* = 17	2.3 ± 0.27	*n* = 8
Head/body length (mm)	572 ± 4.8	*n* = 16	533 ± 2.5	*n* = 8

Ref: Grassman *et al*. (2005a)

Flat-headed cat *Prionailurus planiceps* (Vigors and Horsfield, 1827)

The flat-headed cat takes its name from its unusually long, sloping snout and flattened skull roof, with small ears set well down the sides of its head. It has large, close-set eyes, and relatively longer and sharper teeth than its close relatives (Muul and Lim 1970; Groves 1982). Its claws do not retract fully into their shortened sheaths, and its toes are more completely webbed than the fishing cat's, with long, narrow-footed pads. Muul and Lim (1970), commenting on the cat's feet and other features, characterized it as the ecological counterpart of a semiaquatic mustelid. In captivity, they played for hours in basins of water, and Shigeki Yasuma observed a wild flat-headed cat playing in water (Nowell and Jackson 1996). The stomachs of two dead flat-headed cats contained mostly fish, and also shrimp shells. They may also take birds and small rodents, and have been reported to prey on domestic poultry (Nowell and Jackson 1996). The species is closely associated with wetlands, to a greater degree than the fishing cat, with a much smaller distribution, found only on the islands of Borneo and Sumatra and the Malayan peninsula (Map 34). Most collection records for the flat-headed cat are from swampy areas, oxbow lakes, and riverine forest (Nowell and Jackson 1996). They also occur in peat-swamp forest (Bezuijen 2000), and have been observed in recently logged forest (Bezuijen 2000, 2003; Meijaard *et al.* 2005b). All published observations of live animals have taken place at night, near water (Nowell and Jackson 1996; Bezuijen 2000, 2003; Meijaard *et al.* 2005b). Flat-headed cats are only found in lowland forest, and this habitat is disappearing with cultivation of oil palm,

	Male			Female		
	Mean	Range	Sample size	Mean	Range	Sample size
Weight (kg)	1.9	1.5–2.2	*n* = 5	1.7	1.5–1.9	*n* = 3
Head/body length (mm)	488	446–521	*n* = 6	470	455–490	*n* = 3

Ref: Sunquist and Sunquist (2002)

Map 34 Flat-headed cat. © IUCN Red List 2008.

logging, settlement, agriculture, and aquaculture. The flat-headed cat was upgraded from Vulnerable to Endangered on the IUCN Red List (IUCN 2008).

Rusty-spotted cat *Prionailurus rubiginosus* (I. Geoffroy Saint-Hilaire, 1831)

The world's smallest cat, its common name is taken from the elongated rust-brown spots that stripe the rufous grey fur of its back and flanks. Found only in India and Sri Lanka (Map 35), the rusty-spotted cat is poorly known. In India, it was long thought to be confined to the south, but recent records have established that it is found over much of the country (Sunquist and Sunquist 2002; Patel and Jackson 2005; Manakadan and Sivakumar 2006; Patel 2006; Vyas *et al.* 2007). Rusty-spotted cats occupy dry forest types as well as scrub and grassland, but are likely absent from evergreen forest in India (Nowell and Jackson 1996), although there are a few records from montane and lowland rainforest in Sri Lanka (Deraniyagala 1956; Nekaris 2003). While dense vegetation and rocky areas are preferred (Worah 1991; Kittle and Watson 2004; Patel 2006), rusty-spotted cats have been found in the midst of agricultural and settled areas (Nowell and Jackson 1996; Mukherjee 1998). They are highly arboreal (Sunquist and Sunquist 2002; Patel 2006), although most observations have been on the ground, at night (Mukherjee 1998; Kittle and Watson 2004; Patel 2006; Vyas *et al.* 2007). One cat was seen hunting frogs, but small rodents were the main prey reported from a series of observations by Patel (2006)—seeking out such prey is probably why the cats venture into cultivated areas, where they may interbreed with domestic cats. Outside Sri Lanka's Yala National Park, Kittle and Watson (2004) observed a rusty-spotted cat mating with a domestic cat and also saw a potential hybrid ('being slightly larger in size, with long legs and exhibiting unusual

Map 35 Rusty-spotted cat. © IUCN Red List 2008.

Plate N Rusty spotted cat *Prionailurus rubiginosus* carrying a rat. © Vidya Athreya.

	Male			Female	
	Mean	Range	Sample size	Mean	Sample size
Weight (kg)	0.9	0.8–1.1	$n = 3$	0.9	$n = 1$
Head/body length (mm)	379 ± 37		$n = 6$	363 ± 34	$n = 8$

Refs: Head/body length, Deraniyagala (1956); Weight, Sunquist and Sunquist (2002)

markings on a paler background'). The rusty-spotted cat is classified as Vulnerable on the IUCN Red List of Threatened Species (IUCN 2008).

Fishing cat *Prionailurus viverrinus* (Bennett, 1833)

The fishing cat is well adapted for catching fish, its primary prey (Bhattacharyya 1989; Mukherjee 1989; Haque and Vijayan 1993). It has a deep-chested body, with short legs and tail, and small close-set ears. Like the flat-headed cat, its front feet are partially webbed, and its claw tips protrude from their sheaths even when retracted, thus giving a signature track imprint (Sunquist and Sunquist 2002). It is a strong swimmer and can cover long distances under water (Roberts 1977). Fishing cats are strongly associated with wetland. They are typically found in swamps and marshy areas, oxbow lakes, reed beds, tidal creeks, and mangrove areas. Along watercourses they have been recorded at elevations up to 1525 m, but most records are from lowland areas (Nowell and Jackson 1996). Although fishing cats are widely distributed through a variety of habitat types across Asia (Map 36), their occurrence tends to be highly localized and is still not well known. For example, in 2005, a fishing cat was run over by a vehicle in central India, well outside the known range of the species (Anonymous 2005a). In Sundaland, it has been confirmed to occur only on the island of Java, and is possibly replaced by *P. planiceps* on Borneo, Sumatra, and peninsular Malaysia (Melisch *et al.* 1996). On the island of Sumatra, previously reported camera trap records (Kawanishi and Sunquist 2003) were actually of leopard cats (J. Sanderson, personal communication 2008), and there are no museum specimens (Melisch *et al.* 1996). There is also no confirmed evidence of presence in peninsular Malaysia (Melisch *et al.* 1996; Kawanishi and Sunquist 2003). Fishing cats, unlike most other

Map 36 Fishing cat. © IUCN Red List 2008.

small cats, may prey primarily on fish rather than small mammals. A 1-year study of scats in India's Keoladeo National Park found that fish comprised 76% of the diet, followed by birds (27%), insects (13%), and small rodents last (9%) (Haque and Vijayan 1993). Molluscs, reptiles, and amphibians are also taken (Mukherjee 1989; Haque and Vijayan 1993). However, they are capable of taking large mammal prey, including small chital fawns (Nowell and Jackson 1996; Sunquist and Sunquist 2002), and have been seen scavenging livestock carcasses and tiger kills (Nowell and Jackson 1996). The only radio-telemetry study took place in Nepal's Chitwan National Park in the early 1990s. Cats were active only at night and spent most of their time in dense tall and short grasslands, sometimes well away from water. Home ranges of three females were 4–6 km^2; that of a single male was larger at 16–22 km^2 (J. L. D. Smith, personal communication in Sunquist and Sunquist [2002]). Fishing cats have been observed in degraded habitats, such as near aquaculture ponds with little vegetation outside the Indian city of Calcutta (P. Sanyal, in Anonymous [2005a]). Locally common in some areas in eastern India and Bangladesh (Khan 2004), elsewhere fishing cats have become increasingly hard to find. The scarcity of recent fishing cat records suggests that over the past decade the species has undergone a serious and significant decline, throughout south-east Asia and in parts of India. This is largely attributed to wetland destruction and degradation, but indiscriminate trapping, snaring, and poisoning may also be to blame. Even in protected wetlands and former fishing cat study areas, researchers have been unable to document fishing cat presence (IUCN 2008). The fishing cat was upgraded from Vulnerable to Endangered on the 2008 IUCN Red List.

	Male Mean	Sample size	Female Mean	Sample size
Weight (kg)	16	*n* = 1	5.1–6.8	*n* = 2
Head/body length (mm)	660	*n* = 1	648–743	*n* = 2

Refs: Male, Haque and Vijayan (1993); Females, J. L. D. Smith (personal communication) in Sunquist and Sunquist (2002)

Study of felids

The value people place on wild animals will depend heavily on their knowledge of them and therefore science and the generation of information is itself a contribution to conservation (Macdonald *et al.*, Chapter 29, this volume). Furthermore, conservation action needs to be firmly underpinned by scientific data.

We searched, using all extant genus names as keywords, for felid papers in abstract databases (BIOSIS, CAB Abstracts, and Zoological records) for the years 1950–2008. The keywords searched came up with a total of 2110 published felid papers, 1811 of which mentioned a single felid species, 299 of which dealt with multiple felid species. Here, we use the number of published papers as a proxy for the degree of attention paid to the scientific studies of felids over time, for each species and within each topic within the field. This is surely a rough index of academic endeavour, and it does not include articles from the grey literature or papers to be found outside mainstream English language journals. As there are extensive bodies of knowledge published in other languages, such as Russian, Chinese, and Spanish,

this may lead to some bias; nevertheless, some revealing trends emerge.

Overall, the rate of publication on wild felids has increased from a total of 41 in the 1950s to a total of 115 in the last decade, reflecting the growth of conservation biology and natural sciences in academia. The past 60 years has seen an exponential growth in publications on felid papers in ecology, behaviour, and conservation (Fig. 1.9a and b). More recent trends have seen growth in cutting-edge fields, such as genetics, as new tools and technologies have become available. Of these publications, 74% of papers dealing with human–felid conflict have been published in the past decade, making this the fastest-increasing area of research, perhaps due to a dawning realization that increasing human pressures on the natural world and the resultant conflict presents threats and dangers to wild predators.

While academic study may not necessarily translate to conservation action, it is comforting to note the massive increase in study of wild felids. Nevertheless, there are still lacunae in knowledge. Large species tend to receive more attention (Fig. 1.10a–d). This may be a reflection of their charisma, greater ease of observation, and the greater potential to attract funding to undertake studies on species that are well known and exciting to a wider public. Efforts to foster public knowledge and interest in the smaller, more cryptic, species may correct this imbalance. Equally, it should be acknowledged that there is a strong justification for the attention paid to the large species because of their potential as flagship and umbrella species for protecting natural ecosystems.

Felids in forested habitats tend to be less well studied. This may speak to the logistical difficulties of working and making observations of felid species in closed habitats. The small cats of Asia and South America are relatively poorly known and this is a major gap in knowledge, as close to 45% of extant felids are small (<10 kg) and occur in these two geographic regions. The apparent lack of attention paid to South American felids (Fig. 1.10c) may, in part, reflect a language bias in publications searched. Despite having smaller felid assemblages, greater numbers of field-based studies on felids were found for North America and Europe (Fig 1.10d), reflecting perhaps a longer history of formal publication in the natural sciences and greater resources and funding available for conservation and educational facilities and institutions.

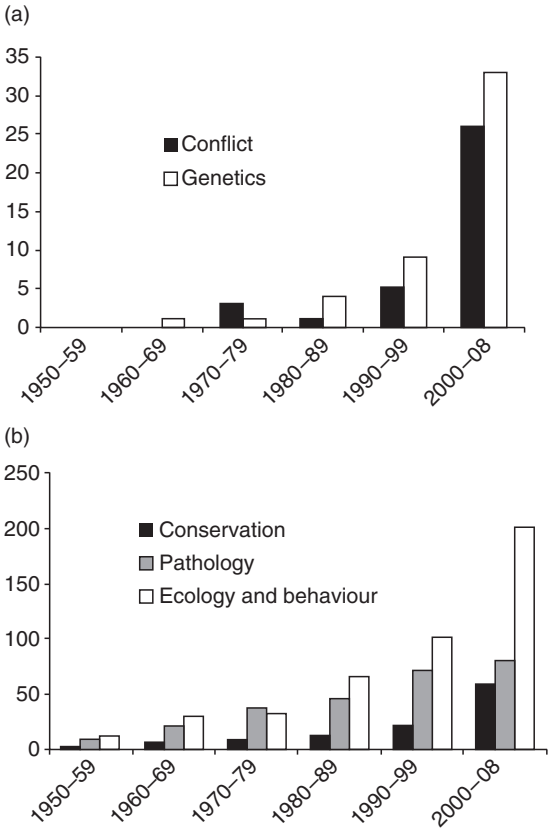


Figure 1.9a and b (a) graph showing increasing number of publications on felids in the fields of genetics and in human–wildlife conflict: both fields have received increasing attention in the last decade; (b) felid publications in conservation, pathology, and ecology/behaviour.

Research effort varies not only geographically, but also in terms of species rarity. To analyse to what extent study effort has prioritized the most threatened species, we used the digital library maintained by the IUCN SSC Cat Specialist Group (www.catsglib.org), which in March 2008 contained 6123 documents pertaining to cats, including peer-reviewed journal articles, an extensive grey literature, as well as non-English materials. However, articles published in the group's biannual newsletter *Cat News* are not included in the database, and so research effort is still under-represented. We looked at

the number of references per species according to their classification on the IUCN Red List of Threatened Species (IUCN 2008).

As previously noted, big cats received predominant emphasis in research effort, with seven large species having twice the number of citations (4065) than the 29 smaller species (2051). However, big cats are relatively more threatened, with four (57%) listed in the top three threat categories, as compared to 38% of the smaller species. Overall, the top three categories of threat (Critically Endangered, Endangered, and Vulnerable) did have a slightly larger number of citations than the two lower threat categories (3192 vs. 2974), despite having fewer species (16 as compared to 20). However, this is largely due to the threatened status of the better-studied big cats. Threatened small cats have received very little research attention, particularly the small cats of south-east Asia. Figure 1.11 shows the uneven nature of study for the top two threat categories; the tiger has received the 'lion's share' of attention, reflecting not only its power of attraction for scientists, but also the extreme challenges its crowded Asian environment poses for conservation of this large predator. While research emphasis on big cats should aid their

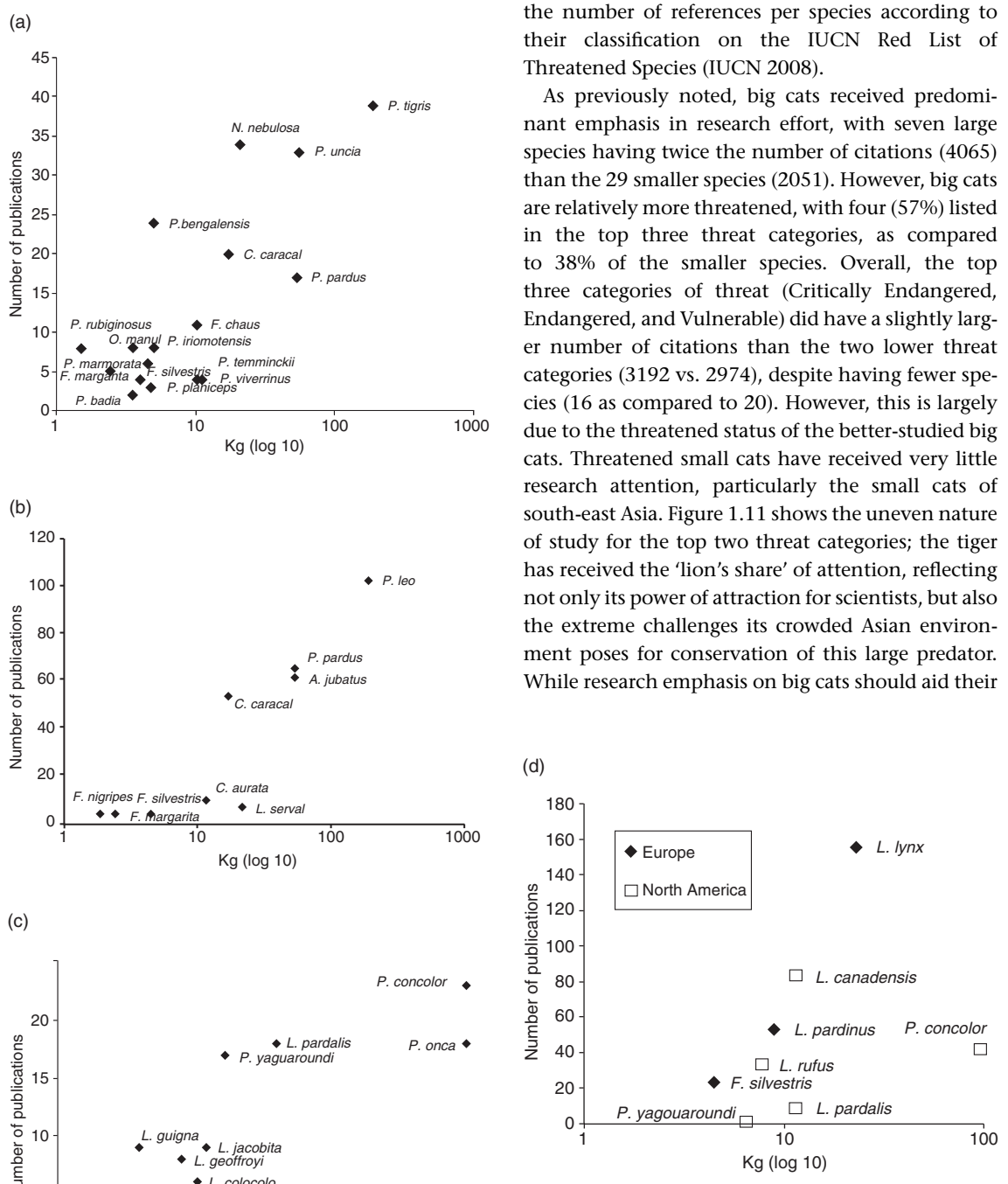


Figure 1.10a–d Publications of field-based studies of felids in (a) Asia; (b) Africa; (c) South America; and (d) North America and Europe, demonstrating that the larger species tend to recieve the most attention, while small-bodied species, particularly those favouring dense habitats tend to recieve less attention.

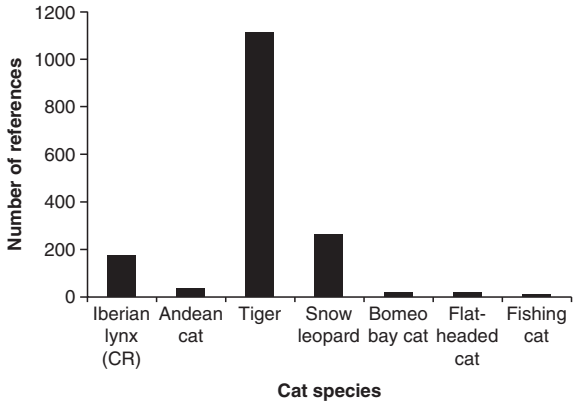


Figure 1.11 Number of references in the Cat Specialist Group library for Critically Endangered (CR) and Endangered cats. The tiger has received a disproportionate focus, although appropriate given its conservation challenges, while research effort for endangered small cats has lagged behind.

conservation, more work on small cats is needed, particularly the rarer species.

As Karanth *et al*. (Chapter 7, this volume) point out, the growth and increasing availability of new technologies and methodologies is likely to open up new and exciting areas of research, some of which will help to fill these gaps. Camera traps and technologies that allow remote recording of the presence and behaviour of cryptic species will illuminate the lives of elusive cats. Advances in genetics are likely to offer insights into the relatedness between species, populations, and individuals.

Finally, there is wide recognition that conservation of predatory species needs to be reconciled with human needs. Wild felids stand out as a family of species that engages our imaginations through their charisma, beauty, and wildness. However, these obligate carnivores also conflict strongly with human needs and activities, engendering equally passionate dislikes by those whose livelihoods they impact. It is crucial that these conflicts are addressed through education, that conservation is wisely planned, and that any utilization is well managed. This requires a broad grasp of relevant knowledge (the subject of the following nine reviews), and the deep insight of case studies (of which we present 18 exceptional examples). It will also require a radical approach to conservation, new heights in interdisciplinarity, and ingenious market mechanisms, and these are some of the strands presented in our concluding synthesis (Macdonald *et al*., Chapter 29, this volume). Just as their precarious position aloft the food pyramid makes felids important umbrella species for conservation—and miners' canaries for biodiversity as a whole—their beauty, cultural significance, and charisma make them potent standard-bearers for nature on the world stage. It is therefore sobering to remember that while it takes whole communities, locally and internationally, to conserve a population of wild felids, it takes just one man with some poison to obliterate them. Therefore, the broad perspective of knowledge-based conservation, integrated with community development and an exhilarating hope for the future, will wither on the vine if local conflicts between people and felids are not resolved. The insights in this book provide the foundation for doing so, and make clear why it will be worth the effort.

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