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The World's Small Carnivores: Definitions, Richness, Distribution, Conservation Status, Ecological Roles, and Research Efforts

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SUMMARY

Small carnivores – here defined as members of the mammalian order Carnivora with a body mass < 21.5 kg – occur worldwide, including in Oceania, following introductions. They are represented by 210 to 282 species, which correspond to about 90% of terrestrial carnivores globally. Some species are endemic to 1 or 2 countries (sometimes only islands), while others, like the red fox, *Vulpes vulpes*, are present in nearly 90 countries over 5 continents. Small carnivores inhabit virtually all of the Earth's ecosystems, adopting terrestrial, semi-fossorial, (semi-)arboreal or (semi-)aquatic lifestyles. They occupy multiple trophic levels, being primary consumers when feeding on fruits, seeds, and other plant matter, secondary consumers when preying on frugivorous, granivorous, and herbivorous animals, or tertiary consumers when killing and devouring meat-eating animals. Therefore, they play important roles in the regulation of ecosystems, e.g. natural pest control, seed dispersal and nutrient cycling. In areas where humans have extirpated large carnivores, small carnivores may become the dominant predators, which may increase their abundance ('mesopredator release') to the point that they can sometimes destabilize communities, drive local extirpations, and reduce overall biodiversity. On the other hand, one-third of the world's small carnivores are Threatened or Near Threatened with extinction (*sensu* IUCN). This results from regionally burgeoning human populations' industrial and agricultural activities, causing habitat reduction, destruction, fragmentation, and pollution. Overexploitation, persecution, and the impacts of introduced predators, competitors, and pathogens have also negatively affected many small carnivore species. Although small carnivores have been intensively studied over the past decades, bibliometric studies showed that they have not received the same attention given to large carnivores. Furthermore, there is a huge disparity in how research efforts on small carnivores have been distributed, with some species intensively studied, and others superficially or not at all. Regionally, North American and European small carnivores have been the focus of numerous studies, and more research is being progressively conducted in Asia. However, there is a need to increase the research effort in Africa and Central and South America. Encouragingly, the recognition of the importance of the mesopredator release effect and the exponential deployment of camera-traps have started to boost the research effort and scientific knowledge on small carnivores around the world. This book aims at filling a gap in the scientific literature by elucidating the important roles of, and documenting the latest knowledge on, the world's small carnivores. It is divided into four main sections: (i) Evolution, Systematics, and Distribution; (ii) Ecology, Behaviour, and Diseases; (iii) Interspecific Interactions and Community Ecology; and (iv) Interactions with People and Conservation. We hope that the book will appeal to a wide audience and, considering that the field of small carnivore science remains wide open, stimulate much-needed research globally.

Keywords

Bibliometric studies — Carnivora — geographic range — phylogeny — taxonomy — threats — systematics

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What is a Small Carnivore?

This edited book focuses on small carnivores. This naturally calls for a definition of 'small carnivores', particularly because these members of the class Mammalia do not form a distinct – or monophyletic – taxonomic unit. As a start, the term 'carnivore' (from the Latin *carne*, meat, and *vorare*, to eat) is used here as a popular synonym of carnivorans, i.e. mammal species belonging to the order Carnivora. Readers should however bear in mind that the latter term, which is based on a phylogenetic classification (Goswami, 2010), is technically more correct and less confusing, as some carnivorans rarely include meat in their diet. For example, the red panda, *Ailurus fulgens*, almost exclusively eats bamboo, and the kinkajou, *Potos flavus*, primarily feasts on fruits. The ancestors of modern-day carnivores were all meat-eaters and had in common the possession of a set of four carnassial teeth – the two fourth upper premolars and the two first lower molars – that would shear through flesh efficiently (Macdonald, 1992). Carnivores have since evolved and colonized a wide range of habitats, with some species progressively changing their diet to mostly feed on plant matter or insects with corresponding morpho-physiological adaptations, including modifications of the carnassial teeth (Ewer, 1973). Similarly, not all meat-eating animals are carnivorans. In fact, the main confusion comes from the fact that the term 'carnivore' can both be used as a synonym of 'carnivoran' (phylogenetic concept) and as an ecological concept (Allaby, 2009), with carnivore then corresponding to the substantive form of the adjective 'carnivorous'. This book, however, does not include other small predator species such as highly carnivorous marsupials, notably several members of the families Didelphidae (endemic to North and South America) and Dasyuridae (found in Australia, Tasmania, Papua New Guinea, and Indonesia). Nonetheless, it is worth mentioning that marsupial carnivores likely play similar ecological roles to those of small carnivorans, and several species of carnivorous marsupials are equally understudied (e.g. Glen & Dickman, 2014).

There is no unanimously accepted definition of what a small carnivore is. Among carnivore biologists involved in conservation and familiar with the specialist groups of the International Union for the Conservation of Nature's Species Survival Commission (hereafter IUCN SSC), small carnivores are implicitly defined as all the terrestrial carnivores that do not belong to the most charismatic carnivore families, namely the cats (Felidae), dogs (Canidae), bears (Ursidae) and hyenas (Hyaenidae). The IUCN SSC possesses specialist groups dedicated to the conservation of each of the above families, while the remaining families have been progressively incorporated into the original Mustelid & Viverrid Specialist Group to form what is currently known as the Small Carnivore Specialist Group. The ensuing corporate definition of small carnivores is obviously arbitrary, especially considering the plethora of small-sized felids and canids that populate the world's ecosystems.

From a purely biological standpoint, there are morphological, ecofunctional, and ecophysiological definitions, and a species considered as a small carnivore by some may be regarded as a medium-sized or even large carnivore by others. The classification may also differ from one ecosystem to another, and vary locally over time, depending on changes in the composition of the carnivore taxocenosis (i.e. a group of sympatric species sharing a common phylogenetic clade). Using body mass as the primary criterion to categorize carnivores, Buskirk (1999) defined mesocarnivores (i.e. medium-sized carnivores) as mammalian predators weighing between 1 and 15 kg. Based on this categorization, only species weighing less than 1 kg would be considered small carnivores, while large carnivores would be those species weighing 15 kg and above (see e.g. Wolf & Ripple, 2018). Other authors regard mesocarnivores (or mesopredators) as small- and mid-sized species weighing less than 15 kg (Roemer *et al.*, 2009), which itself brings confusion to the debate, as this definition disregards the very meaning of the prefix *meso-* which refers to middle or intermediate body size or mass. In contrast, the latter definition is interpreted literally when a species such as the cheetah, *Acinonyx jubatus* (with an adult body mass of 20–65 kg) is defined by some authors as a 'mesopredator' in comparison to the much larger African lion, *Panthera leo* (110–270 kg) (Gigliotti *et al.*, 2020). This raises the question as to which upper body mass threshold should ideally be selected to define mesocarnivores, seeing that other studies rather regard the cheetah as belonging to the African large predator guild (Rafiq *et al.*, 2020) and

prefer to focus on the dominant versus subordinate roles played by these predators in interspecific interactions (Marneweck *et al*., 2019).

Ecologically, carnivores can occupy a broad range of trophic levels (see Fleming *et al*., 2017 for a review focusing on canids). Although most of them are secondary consumers feeding mainly on herbivorous, frugivorous, and granivorous animals, some are essentially primary consumers feeding on plant matter, fruit, and seeds (Hunter & Barrett, 2018). Further, it is not uncommon for others to act as tertiary or even quaternary consumers (e.g. grass → rodent → first-order carnivore → second-order carnivore → third-order carnivore). For example, Yang *et al*. (2018) found that up to six mid-sized carnivore species were predated by Amur tigers, *Panthera tigris altaica*, and Amur leopards, *Panthera pardus orientalis*. Therefore, because carnivores also feed on each other (intra-taxocenosis or even intraguild predation), the available behavioural and dietary data suggest that the three following ecofunctional categories could be considered: (i) species who never kill and consume other carnivore species, but who fall prey to larger-sized carnivores; (ii) species who kill and consume other carnivore species and are themselves predated by other carnivores; and (iii) species who kill and occasionally consume other carnivore species, but whose adult individuals (contrarily to young) are not usually killed by other carnivore species. Due to subduing imperatives, these categories would imply that the corresponding members of these trophic levels are of small, medium, and large sizes, respectively. However, body size and mass are not the only factors that determine the occurrence and outcome of such predatory interactions, and the range of carnivore body sizes and masses will vary depending on the local taxocenosis. As a result, body mass thresholds between these three ecological groups of carnivores are not discrete, and, therefore, difficult to determine precisely.

Ecophysiological considerations can provide scientific grounding for categorizing carnivores into body mass groups. Carbone *et al*. (1999) noted a dichotomy in terrestrial carnivore diets, with smaller species feeding on invertebrates and small vertebrates generally weighing less than half their body mass; and larger species essentially preying on large vertebrates that are near their mass. These authors suggested that although intake rates of invertebrate feeders are low, small carnivores could subsist on such a diet because invertebrates constitute a superabundant resource in most ecosystems, and small carnivores have low absolute energy requirements. For larger carnivores, however, invertebrate feeding appears to be unsustainable. Using a simple energetic model and known invertebrate intake rates, Carbone *et al*. (1999) predicted a maximum mass of 21.5 kg above which feeding on small prey is unsustainable. In a follow-up study, Carbone *et al*. (2007) showed that the transition from small to large prey can be predicted by the maximization of net energy gain. While their improved model showed that small prey can sustain carnivores weighing up to 18–45 kg, carnivores weighing above 14.5 kg will achieve a higher net gain by feeding on larger prey. The shift from small to large prey is, therefore, expected and indeed observed in a body mass range of roughly 15–21 kg, depending on the species, season, and location. A recent study that investigated the relationship between stomach capacity and pack-corrected prey mass (i.e. the amount of food available for each member of the predator 'hunting group') confirmed the existence of two main carnivore functional groups, namely small-prey feeders and large-prey feeders (De Cuyper *et al*., 2019). The majority of large-prey feeders are above, and of small-prey feeders below, a body mass of 10–20 kg. However, both functional groups occur across the whole body mass spectrum, suggesting that the dichotomy might not only be determined by physiology, but also by ecological factors related to body size.

In order to select the species to consider for this book as a whole, we, therefore, decided to define small carnivores as members of the order Carnivora whose average body mass is below 21.5 kg (see species list and average body masses in Appendix A). We, however, acknowledge that because the shift from small to large prey can take place over a large range of body masses, some species weighing between 15 and 21 kg may warrant being regarded as large carnivores. Similarly, the giant otter, *Pteronura brasiliensis*, and the sea otter, *Enhydra lutris*, are considered here as large carnivores based on their average body mass (28 and 30 kg, respectively; Hunter & Barrett, 2018), even though they feed on comparatively small prey (10–40 cm long fish and marine invertebrates, respectively). Living in

aquatic and marine environments could possibly complicate access to larger prey – in terms of availability, catching, and subduing – as opposed to what is the case in terrestrial systems. Giant otters are, however, capable of taking large turtles, > 1 m long catfish, caimans to 1.5 m and anacondas to 3 m (Hunter & Barrett, 2018). The case of some bears feeding almost exclusively on plants (e.g. giant panda, *Ailuropoda melanoleuca*) or termites, ants, and fruits (e.g. sloth bear, *Melursus ursinus*) is more puzzling, and this is clearly food for thought for evolutionary biologists and nutritional ecologists (Nie *et al*., 2019; Jiangzuo & Flynn, 2020). Hence, due to the above-mentioned hurdles and the lack of a current consensus on what a small carnivore is, we have not imposed this definition upon the contributors. As a result, the individual chapters may follow any of the approaches mentioned above, or be based on different body mass thresholds.

This book does not include contributions on any of the 36 species of marine carnivores (Wozencraft, 2005) belonging to the Phocidae (seals), Otariidae (sea lions), and Odobenidae (walrus, *Odobenus rosmarus*) families whose representatives weigh between 90 and 3600 kg and feed on a different range of primarily aquatic prey (Reeves *et al*., 2002). Due to their shared morphological and ecological characteristics, these aquatic species were previously considered to form an order on their own, the Pinnipedia; however, elevating pinnipeds to the order rank would make the Carnivora an incomplete systematic unit, a so-called paraphyletic taxon (Flynn *et al*., 2005; Sato *et al*., 2006).

Although the term 'terrestrial' is used here to qualify all members of the order Carnivora outside the Pinnipedia (previously called the Fissipedia), some terrestrial species are largely aquatic (e.g. otters; otter civet, *Cynogale bennettii*) or may forage in shallow waters (e.g. water mongoose, *Atilax paludinosus*, crab-eating mongoose, *Urva urva*, aquatic genet, *Genetta piscivora*, crab-eating raccoon, *Procyon cancrivorus*, fishing cat, *Prionailurus viverrinus*, and brown bear, *Ursus arctos*) (Garshelis, 2009; Jennings & Veron, 2009; Kays, 2009; Larivière & Jennings, 2009; Gilchrist *et al*., 2009; Sunquist & Sunquist, 2009). Other species are partly (e.g. martens, *Martes* spp.; genets, *Genetta* spp.; fosa, *Cryptoprocta ferox*; several bear species) to chiefly or exclusively arboreal (e.g. palm civets; oyans and linsangs; binturong, *Arctictis binturong*; olingos, *Bassaricyon* spp.; sun bear, *Helarctos malayanus*), while Eurasian badgers *sensu lato*, *Meles* spp., and American badger, *Taxidea taxus*, can be regarded as semi-fossorial, as they dig extensive burrows where they spend a significant proportion of their life (Garshelis, 2009; Gaubert, 2009a,b; Goodman, 2009; Jennings & Veron, 2009; Kays, 2009; Larivière & Jennings, 2009; Proulx *et al*., 2016).

Phylogeny and Number of Families

The scientific revolution created by the advent of molecular biology has enabled taxonomists, systematists, and phylogeographers to shed light on the genetic relationships between extant taxa. These methods have assisted in fine-tuning the phylogenetic tree of the order Carnivora (Figure 1.1). It now regroups 13 terrestrial families; Ursidae does not contain any small carnivores, while several others are comprised entirely of small carnivores (Figure 1.1).

Recent progress in molecular phylogenetics has since revealed the well-resolved carnivoran phylogeny in both major clades of Caniformia ('dog-like' species) and Feliformia ('cat-like' species) to the extent that little remains to be enlightened on the interfamilial relationships. During the last decade or so, the supermatrix approach with nuclear gene sequences under the probabilistic phylogenetic criteria has contributed greatly to the clarification of some enigmatic phylogenetic relationships; e.g. Eupleridae: Yoder *et al*. (2003); Prionodontidae: Gaubert & Veron (2003); Pinnipedia and Ursidae: Flynn *et al*. (2005) and Sato *et al*. (2006); Ailuridae and Mephitidae: Sato *et al*. (2009). In addition to the phylogenetic topological issues, the divergence times among families have also been largely consistent among studies which adopted different fossil calibrations, especially those using mainly nuclear gene sequences (Koepfli *et al*., 2006; Sato *et al*., 2009; Eizirik *et al*., 2010; Fulton & Strobeck, 2010; Meredith *et al*., 2011). Figure 1.1 shows the currently accepted phylogenetic relationships among families within the order Carnivora, where the divergence times among them were calculated from arithmetically averaging the estimates in the above-mentioned studies. These are based on the taxon-by-characters supermatrix

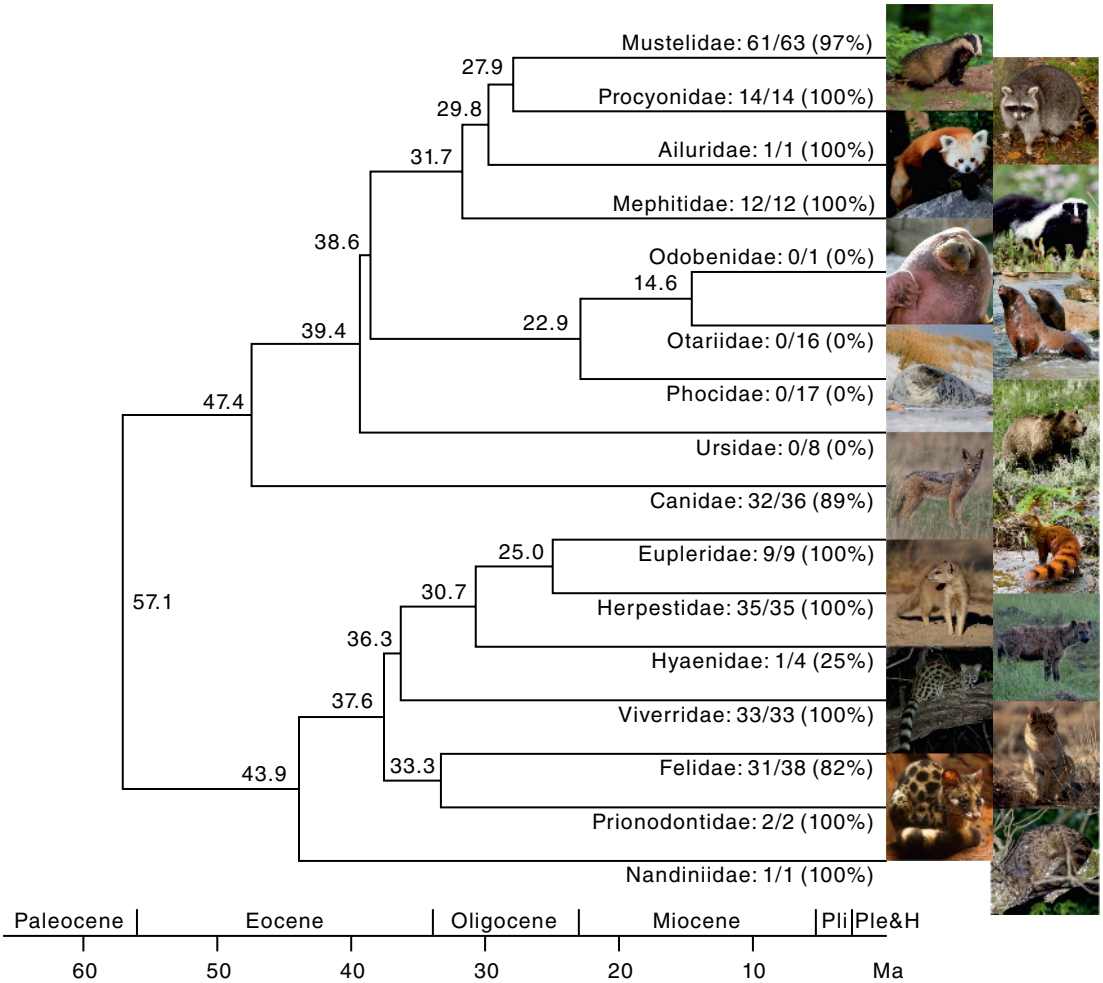


Figure 1.1 Phylogenetic relationships among the 16 families within the order Carnivora summarized on the basis of the estimates in recent molecular phylogenetic studies using the taxon-by-characters supermatrix mainly consisting of more than 5000 bp nucleotide sequences from multiple nuclear genes. Divergence times were arithmetically averaged based on estimates provided in the literature (see references in the text). The percentage proportions of the small carnivores (< 21.5 kg; $n = 232$) in each family are indicated after the family names. Pli = Pliocene, Ple = Pleistocene, H = Holocene. *Source:* Photos © Pascal Gérold (European badger, *Meles meles*), Steven Jansen (northern raccoon, *Procyon lotor*; grey seal, *Halychoerus grypus*), Jacob Dingel (striped skunk, *Mephitis mephitis*), Alex Sliwa (red panda, *Ailurus fulgens*; walrus, *Odobenus rosmarus*; Steller sea lions, *Eumetopias jubatus*; brown/grizzly bear, *Ursus arctos*), Emmanuel Do Linh San (black-backed jackal, *Canis [= Lupullela] mesomelas*; yellow mongoose, *Cynictis penicillata*; spotted hyaena, *Crocuta crocuta*; African wild cat, *Felis lybica*), Nick Garbutt @ www.nickgarbutt.com (ring-tailed vontsira, *Galidia elegans*), Len de Beer (rusty-spotted genet, *Genetta maculata*), Johannes Pfleiderer (Spotted linsang, *Prionodon pardicolor*), and David Mills (African palm civet, *Nandinia binotata*).

consisting of more than 5000 bp nucleotide sequences from multiple nuclear genes. Most of the divergence among families occurred from the middle Eocene to the late Oligocene. Only the marine pinniped families started the diversification in the Miocene. The number of subfamilies within the order Carnivora is still debated and likely to change with future studies.

Number of Species, 'New' Species, and Taxonomic Uncertainties

The number of small carnivore species worldwide is dependent upon both the definition used as well as the handling of several cases of taxonomic uncertainty present within this mammalian order. An in-depth

look at species lists in recent compendia on carnivores suggests that the species rank attributed to 233 taxa of terrestrial carnivores is not in dispute. Recent sources list between 245 and 251 carnivore species, and species composition slightly varies among them (Nowak, 2005; Wozencraft, 2005; Wilson & Mittermeier, 2009; Hunter & Barrett, 2011, 2018; Table 1.1). During its 2015/2016 reassessment of the conservation status of carnivores worldwide, the IUCN listed 255 terrestrial carnivore species. However, as more work is completed, additional species are likely to be recognized. For example, the African wolf, *Canis lupaster*, was recently recognized and assessed following a series of research works filled with twists and turns (IUCN, 2021; see other references in Appendix B). Two additional cat species were recognized – but not yet assessed – in 2017 after a thorough and much-needed revision of the taxonomy of the Felidae (Kitchener *et al*., 2017). A detailed review of the literature indicates that at least an additional 51 taxa, for a total of 309, were claimed, suggested or convincingly demonstrated by some authors to warrant species status (see contentious cases for small carnivores in Appendix B). Domestic and feral carnivores constitute a separate and complex case, which will not be debated here (see Wyrwoll, 2003; Gentry *et al*., 2004). Considering that there are 23 to 27 large terrestrial carnivore species globally, the number of small carnivore species could,

Table 1.1 Number of extant terrestrial carnivore species recognized by five recent standard references, and number of species in each family.

Suborders and families[a]	Nowak (2005)	Wozencraft (2005)	Wilson & Mittermeier (2009)	Hunter & Barrett (2011)	Hunter & Barrett (2018)	IUCN (2021)	% IUCN (2021)
Caniformia							
Mustelidae	67	58	57	56	60–62	63	**24.6**
Procyonidae	19[b]	14	12	13	13	14	**5.5**
Ailuridae	—[c]	1	1	1	1	1	**0.4**
Mephitidae	—[d]	12	12	12	11	12	**4.7**
Ursidae	8	8	8	8	8	8	**3.1**
Canidae	35	34	35	35	35	35	**13.7**
Feliformia							
Eupleridae	–[e]	8	8	9	7	9	**3.5**
Herpestidae	39	33	34	34	34	35	**13.7**
Hyaenidae	4	4	4	4	4	4	**1.6**
Viverridae	35	35	34	33	33	33	**12.9**
Felidae	38	40	37	37	40	39	**15.2**
Prionodontidae	—[f]	—[f]	2	2	2	2	**0.8**
Nandiniidae	—[g]	1	1	1	1	1	**0.4**
Total	**246**[a]	**248**	**245**	**245**	**249–251**	**256**	**100.0**

The percentage of species in each family as per IUCN (2021) is provided in the last column. See Figure 1.1 for the numbers and percentages of small carnivore species in each family.

[a] For comparative purposes, families are listed in the same order as that provided in Figure 1.1.

[b] This count included the extinct Barbados raccoon, *Procyon gloveralleni*, as well as several other insular populations of the introduced northern raccoon, *P. lotor*; all of those are currently regarded as insular forms or subspecies at best (see Appendix B).

[c] The red panda, *Ailurus fulgens*, was then classified with the Procyonidae (see Sato & Wolsan, Chapter 2, this volume).

[d] The skunks were previously considered as a separate subfamily (Mephitinae) within the Mustelidae.

[e] The Malagasy carnivores were then regarded as direct relatives of mongooses (Herpestidae) and civets (Viverridae) (see Veron *et al*., Chapter 3, this volume).

[f] The Asian linsangs were formerly classified with the Viverridae. The African linsangs (oyans) are still included in the Viverridae.

[g] The African palm civet, *Nandinia binotata*, was then classified with the Viverridae.

therefore, range from 210 (90.1% of 233 species) to 282 species (91.3% of 309 species). At present, the IUCN (2021) recognizes 232 small carnivore species (90.6% of 256 carnivore species; see full species list in Appendix A), an approach that we have adopted here in view of showing the general trends in the conservation status of small carnivores worldwide. The recognized species are dominated by 5 families: Mustelidae (61 species; 26.3%), Herpestidae (35; 15.1%), Viverridae (33; 14.2%), Canidae (32; 13.8%), and Felidae (31; 13.4%) (Figure 1.1). The remaining 7 families comprise only 40 species, a mere 17.2% of all small carnivore species worldwide.

At least three species of small carnivores have gone extinct over the past centuries – the Falkland Island wolf, *Dusicyon australis*, his continental sister taxon, *D. avus*, and the sea mink, *Mustela macrodon* (Nowak, 2005; IUCN, 2021). However, very few of the recently named species have, in fact, been newly discovered; the validity of others can be questioned. For example, Durbin *et al.* (2010) reported on the discovery of Durrell's vontsira, *Salanoia durrelli*, from the marshes of Lac Alaotra, in Madagascar. This taxon diverged from brown-tailed vontsira, *Salanoia concolor*, in terms of craniodental morphometrics, but exhibited low genetic differentiation at cytochrome *b*. Recent studies by Veron *et al.* (2017) based on mitochondrial and nuclear markers and additional phenotypic characteristics strongly support the existence of a single species within the genus *Salanoia*. Similar cases of rescinded discoveries are reported in Appendix B. A few years ago, Helgen *et al.* (2013) undertook a comprehensive taxonomic revision of the Neotropical olingos. In the process, these authors came to describe a new species, the olinguito, *Bassaricyon neblina*, endemic to the Andes of Colombia and Ecuador. Although this species was newly named, several specimens had previously been collected and misidentified as northern olingo, *Bassaricyon gabbii*. The above-mentioned study has now shown that *B. gabbii* occurs only in Central America.

Perhaps the only recent field discovery of a small carnivore species is the Vietnam ferret badger, *Melogale cucphuongensis*, for which two individuals were found in 2005 and 2006 in Cuc Phuong National Park. Both morphological and cytochrome *b* data pointed to a clear distinction from the two other sympatric ferret badger species (Nadler *et al.*, 2011). However, it is not impossible that this taxon has previously been described under another name and considered synonymous to that of one of the two continental ferret badger species. Clearly, more samples of this newly described taxon would need to be collected and a thorough revision of this genus undertaken. Similarly, the 'discovery' of Lowe's otter civet, *Cynogale lowei*, was based on a single specimen collected in the winter of 1926–1927 in northern Vietnam. Ninety years later, Roberton *et al.* (2017) using microscopic hair and DNA analyses, showed that the type specimen was, in fact, a juvenile Eurasian otter, *Lutra lutra*, thereby refuting the existence of Lowe's otter civet!

The apparent increase in the number of small carnivore species over the past 15 years is primarily due to taxonomic splitting of species. For example, the three to four species of Eurasian badgers *sensu lato* currently recognized result from a progressive split of *Meles meles* (European badger); similarly, the three species of Asian hog badgers, *Arctonyx* spp., were previously considered a single species (see review in Sato, 2016 and references in Appendix B). More generally, a combination of morphological and molecular studies based on a broad range of genetic markers, sometimes coupled with an analysis of biogeographic data, have provided strong evidence for the upgrading or subsuming of some taxa (Appendix B). Several cases are still disputed and require further investigations (Appendix B). It is likely that genome-wide analyses will help clarify the taxonomic rank of several taxa in the near future, as already demonstrated in recent studies (e.g. Koepfli *et al.*, 2015; Gopalakrishnan *et al.*, 2018; Hu *et al.*, 2020).

Geographic Distribution

Small carnivores are present worldwide, with the exception of Antarctica. They occur in Oceania following successful introductions: the red fox, *Vulpes vulpes*, in Australia (including Tasmania) and New Zealand; the stoat, *Mustela erminea*, the least weasel, *M. nivalis*, and the European polecat, *Mustela putorius*, and/or domestic ferret, *M. furo*, in New Zealand; the small Indian mongoose, *Urva auropunctata*, in Hawaii and Fiji; and the Indian brown mongoose, *Urva fusca*, in Fiji. Gantchoff *et al.* (Chapter 20, this volume) report

on some of those successful introductions, as well as on the introduction efforts that failed.

Asia (42%) and Africa (37%) both host large proportions of the world's 232 small carnivore species, followed by Central and South America (22%). Species richness is much lower in North America (16%) and Europe (10%). Most small carnivore species ($n = 185$ or 80%) occur on one continent only and, therefore, analyses which take into account the remaining 20% of species present on two or more continents yield similar proportions (Figure 1.2). The red fox and the small Indian mongoose are present on five continents (islands included), while the stoat, least weasel, European polecat, American mink, *Neovison vison*, and northern raccoon, *Procyon lotor*, occur on four continents, all partially due to introductions.

Although countries differ drastically in surface area, a simple plot of the number of species that occur in a specific number of countries show that pairs of data fall on or very close to the indicated power regression curve (Figure 1.3). No less than 35 species (15%) are endemic to a single country, and among those, 21 (9%)

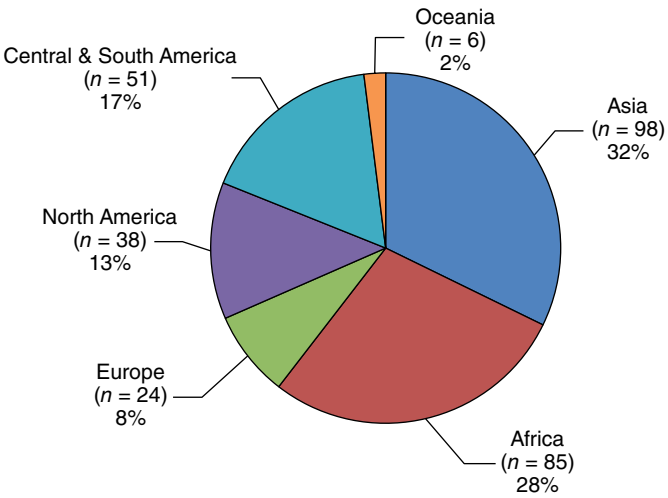


Figure 1.2 Proportional geographic distribution of the 232 small carnivores (< 21.5 kg) recognized by the IUCN (2021). Note that some species occur on two or more continents and are, therefore, counted multiple times ($n = 302$ occurrences). For the purpose of our analysis, Africa includes Madagascar and the nearby Indian Ocean and Atlantic Ocean islands; Central America includes the Caribbean Islands; Oceania comprises Australasia, New Zealand, Polynesia, Melanesia, and Micronesia.

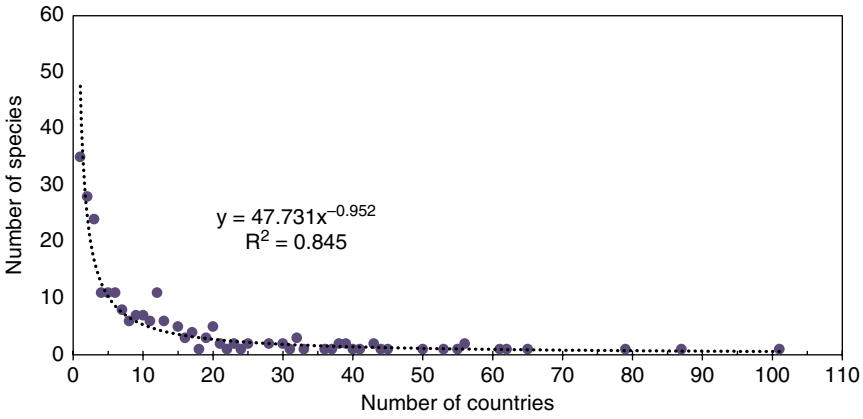


Figure 1.3 The relation between the number of small carnivore species (< 21.5 kg) and the number of countries in which they occur worldwide. The black dotted line represents a fitted power function regression curve. Note that the dot with 101 countries corresponds to *Felis silvestris*. This species has now been split into two, with the European wild cat, *F. silvestris sensu stricto*, present in 34 countries, and the African wild cat, *F. lybica*, in 67 countries occurring from South Africa to China and southern Mongolia.

are island endemics – albeit sometimes present on several islands. Overall, about half of the small carnivore species are present in five or fewer countries, and nearly two-thirds occur in ≤ 10 countries. The remaining one-third consists of species whose distribution spans from 11 to 65 countries. The red fox and the Eurasian otter top the list with 87 and 79 countries, respectively (see caption of Figure 1.3 for the special case represented by the wild cat, *Felis silvestris*).

Conservation Status in an Era of 'Species Inflation'

The latest update of the assessment of the conservation status of small carnivores by IUCN (2021) indicates that about 64% of the 232 species assessed are not currently a source of immediate concern (Figure 1.4; see the full list in Appendix A). Six species (2.6%) could not be assessed due to a deficiency of relevant data; these are three African (Pousargues's mongoose, *Dologale dybowskii*; Ethiopian genet, *Genetta abyssinica*; king genet, *G. poensis*) and three Asian species (Vietnam ferret badger; Sichuan weasel, *Mustela russelliana*; Tonkin weasel, *M. tonkinensis*). Some data have been recently collected on two of these species (D'Haen, 2017; Ferguson *et al.*, 2019), however, while a step in the right direction, the information available is still insufficient to allow a proper evaluation of their conservation status. The remaining one-third of species are Near Threatened (~11%) or threatened *sensu lato* (~23%). Among the latter, 23 species (~10%) are Endangered or Critically Endangered (Table 1.2). Irrespective of their conservation status, only 27% of the world's small carnivore species have stable populations, whereas a mere 3.4% are increasing. In contrast, 50% of the small carnivore species are currently experiencing population declines, and the trends for the remaining 20% are unknown.

While the Earth is currently facing what some call a 'sixth mass extinction' due to human activities (Ceballos *et al.*, 2010, 2015, 2017), the threats to small carnivores result from hunting and fishing (including deadly by-catches), poaching (often with snares), and persecution which directly reduce small carnivore population sizes (Gray *et al.*, 2018; IUCN, 2021). In addition, industrialization, urbanization, and the expansion of agricultural activities cause the reduction, destruction, fragmentation, and pollution of habitats (see review in Marneweck *et al.*, 2021). In this context, deforestation remains one of the most severe threats to forest-dependent species (Püttker *et al.*, 2020; Rocha *et al.*, 2020). Scenarios based on future land-use change predict that several carnivore species, including small carnivores, will be negatively affected (di Minin *et al.*, 2016). Road-traffic mortality may also severely impact some species or populations. Viruses and organisms (from bacteria to mammals)

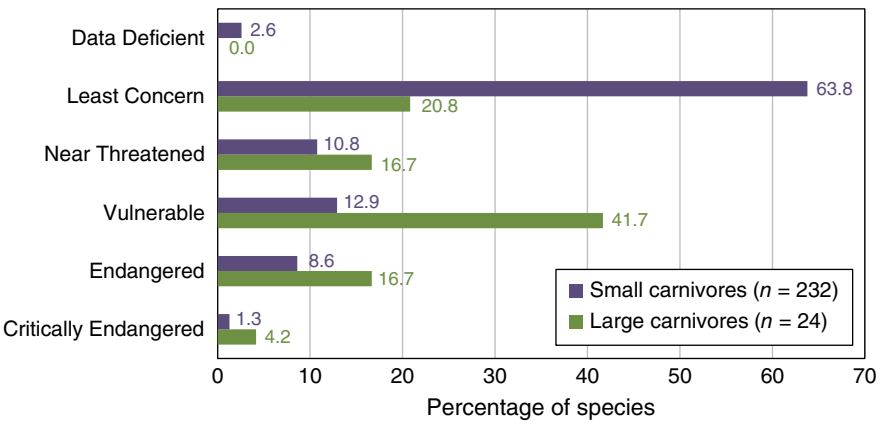


Figure 1.4 *IUCN Red List* categorization of the world's small carnivores (< 21.5 kg) in comparison with that of large carnivores, as assessed majoritarily in 2015 and 2016 (IUCN, 2021).

Table 1.2 A list of the 23 small carnivore species (< 21.5 kg) which are currently listed as Endangered (EN) or Critically Endangered (CR) by the IUCN based on assessments mostly carried out in 2015 and 2016 (IUCN, 2021).

Family and scientific name[a]	Common name	Distribution	*IUCN Red List* categorization	Main threats/concerns (Asssessors/reference)
Ailuridae				
Ailurus fulgens	Red panda	Bhutan, China, India, Myanmar, Nepal	EN	Relatively high forest loss rate and poor survival in fragmented areas – as the species is dependent on bamboos which are vulnerable in deforested/degraded habitats. High susceptibility to canine distemper. Increase in poaching and live-capture for trade (body parts, pelts, pets). Growing human population and encroachment in red panda habitat (herding, bamboo used for fodder, collection of firewood) (Glatston *et al.*, 2015).
Canidae				
Canis simensis	Ethiopian wolf	Ethiopia	EN	Small population size (~400 adults in seven isolated mountain enclaves). Susceptibility to rabies and canine distemper. Afroalpine range shrinking and increasingly fragmented (Marino & Sillero-Zubiri, 2011).
Cuon alpinus	Dhole	Asia (20 countries)	EN	Depletion of prey base, persecution due to livestock predation, habitat loss, disease transmission from domestic dogs, and possibly interspecific competition. Between 4500 and 10 500 individuals distributed in small and isolated subpopulations, often exhibiting severe fluctuations in numbers (Kamler *et al.*, 2015).
Lycalopex fulvipes	Darwin's fox	Chile	EN	Forest loss and risk of contracting canine distemper from domestic dogs. Population size likely does not exceed 2500 individuals (Silva-Rodríguez *et al.*, 2016).
Eupleridae				
Eupleres major[b]	Western falanouc	Madagascar*	EN	Numerous synergistic threats: widespread hunting, persecution, ongoing habitat conversion and fragmentation, and predation by feral cats and domestic dogs (Hawkins, 2016).
Galidictis grandidieri[c]	Grandidier's vontsira	Madagascar*	EN	Habitat loss and fragmentation, and predation by non-native predators. Population estimate is 3000–5000 individuals. Extent of occurrence comprises a single location and is well below 5000 km^2 (may be as low as 1500 km^2) (Hawkins, 2015a).
Mungotictis decemlineata	Bokiboky	Madagascar*	EN	Widespread and increasing habitat loss and degradation, hunting, persecution, and negative impacts of introduced carnivores (Hawkins, 2015b).

Table 1.2 (Continued)

Family and scientific name[a]	Common name	Distribution	*IUCN Red List* categorization	Main threats/concerns (Asssessors/reference)
Felidae				
Catopuma badia	Borneo bay cat	Borneo (Indonesia, Malaysia)*	EN	Hunting believed to potentially have a considerable impact. Species prone to untargeted snaring and evidence of capture and export of animals for the pet trade. Area of occupancy estimated to have decreased by 30% between 2000 and 2010 as a result of ongoing forest loss and conversion to oil palm plantations. The smaller protected areas are fragmented and isolated, hence ineffective in conserving such a low-density species (Hearn *et al*., 2016).
Leopardus jacobita	Andean cat	Argentina, Bolivia, Chile, Peru	EN	Occurs at low densities in patchy rocky habitats associated to wetlands/shrublands. Population estimate is ~2800 individuals. Locally killed by herders (in retaliation for predation) or hunted. Increasing habitat loss and degradation due to expansion of agricultural activities, inadequate livestock management and water extraction. The growing mining and petroleum/gas industry is also of concern (Villalba *et al*., 2016).
Lynx pardinus	Iberian lynx	Spain, Portugal	EN	Only 156 mature individuals in two subpopulations in 2012, with a total area of occupancy of 1040 km^2. Improved status from CR to EN due to intensive, ongoing conservation actions. At least 1111 individuals in several subpopulations in 2020, but affected by car hits (34 in 2019) and illegal hunting. Future range expansion and population increase highly dependent upon continued reintroductions and maintenance of prey base (mostly rabbits) under epizootic and climate change scenarios (Rodríguez & Calzada, 2015).
Prionailurus planiceps	Flat-headed cat	Brunei, Indonesia, Malaysia, Thailand	EN	Restricted and patchy distribution around wetlands. Wetland destruction/degradation (draining for agriculture; pollution; excessive fishing, hunting, and wood-cutting; clearance of coastal mangroves) and the very high deforestation rate are, therefore, the primary threats. Population size is plausibly < 2500 mature individuals (Wilting *et al*., 2015a).
Mustelidae				
Lontra felina	Marine otter	Argentina, Chile, Peru	EN	Original range decreased substantially following excessive hunting. Distribution along the Pacific coast is now restricted and patchy, with fragmentation caused by poaching, pollution, and increased human occupation along the seashores. Accidental kills in crab pots reported. Inferred future population decline due to habitat loss and exploitation (Valqui & Rheingantz, 2015).

(*Continued*)

Table 1.2 (Continued)

Family and scientific name[a]	Common name	Distribution	*IUCN Red List* categorization	Main threats/concerns (Asssessors/reference)
Lontra provocax	Southern river otter	Argentina, Chile	EN	Original range decreased drastically due to habitat destruction (including removal of vegetation), river and stream canalization, and extensive dredging. Poaching and predation by domestic dogs occasionally reported. Projected population decline of ~50% over the 30 years following the assessment due to accelerated habitat destruction and degradation (for otters using freshwater habitats) and the impacts of intensive fishery activities (for marine otters) (Sepúlveda *et al*., 2015).
Lutra sumatrana	Hairy-nosed otter	Cambodia, Malaysia, Thailand, Vietnam	EN	Loss of > 50% of the population during the 30 years preceding the assessment caused by illegal trade-driven hunting (meat, medical use, pets), by-catch, pollution and prey depletion due to overfishing. Current decline rates suspected to continue into the future due to burgeoning human population and growing pressure on natural resources (Aadrean *et al*., 2015).
Melogale everetti	Bornean ferret badger	Borneo (Malaysia)*	EN	Small extent of occurrence (4200 km^2) and area of occupancy (1100 km^2) in two to three locations. Species is rare even in its core range, and possibly threatened by the ongoing land-cover transformations. Climate change on Borneo is projected to particularly threaten highland species such a *M. everetti* because potential upslope range shifts would be impossible (Wilting *et al*., 2015b).
Mustela lutreola	European mink	Estonia, France, Romania, Russian Federation, Spain, Ukraine	CR	Loss of > 50% of the population in the 10 years preceding the assessment. Predicted to intensify to reach a decline rate > 80% in the following 10 years due to habitat degradation/loss and the effects of introduced species, notably the American mink, *Neovison vison*. Western populations (France and Spain) have a very low genetic variability. Genetic introgression (0.9%) following hybridization (3%) with European polecat, *M. putorius*, occur at low levels (Maran *et al*., 2016).
Mustela nigripes	Black-footed ferret	USA, Mexico	EN	Extirpated from most of its former range (from northern Mexico to southern Canada) mainly as a result of prairie-dog, *Cynomys* spp., control programmes and sylvatic plague (exotic disease introduced to the wild population). Today occurs in the wild as 17–22 reintroduced, small, and restricted populations which are intensively managed. Four of those are self-sustaining (all in USA) and have a combined range > 500 km^2. Only ~300 wild-born mature individuals in 2015, with two-thirds in the viable populations (Belant *et al*., 2015).

Table 1.2 (Continued)

Family and scientific name[a]	Common name	Distribution	*IUCN Red List* categorization	Main threats/concerns (Asssessors/reference)
Procyonidae				
Nasuella meridensis	Eastern mountain coati	Venezuela (Andes)	EN	Very small known extent of occurrence (770 km^2) with only five confirmed and spatially aggregated locations. Slight but ongoing loss of cloud forests and Paramo habitats leading to population decline (González-Maya & Arias-Alzate, 2016).
Procyon pygmaeus[d]	Pygmy raccoon	Mexico (Cozumel Island)*	CR	Small population (~190–570 mature individuals) confined to Cozumel Island (488 km^2). Although population size is likely to fluctuate, the overall trend is a rapid decline caused by ongoing human encroachment (urban growth, development, tourism) into the remaining habitat fragments, invasive predators and pathogens, road network expansion and the increasing magnitude/severity of hurricanes (Cuarón *et al.*, 2016).
Viverridae				
Chrotogale owstoni	Owston's civet	China, Lao, Vietnam	EN	Dramatic population decline (> 50%) due to overexploitation, with habitat fragmentation exacerbating the speed at which this civet is extirpated. Exposed to high levels of snaring and other forms of ground-level trapping. Wider occurrence in montane forest and karstic areas, into which industrial snaring has not yet widely spread (Timmins *et al.*, 2016a).
Cynogale bennettii	Otter civet	Brunei, Indonesia, Malaysia, Thailand	EN	Primary habitat (forested, lowland wetlands) and population have declined by ≥ 20% in the 10 years preceding the assessment. Remaining habitat is discontinuous and habitually degraded. Water sources are often polluted. Snaring is also a threat. Population size is plausibly < 2500 mature individuals (Ross *et al.*, 2015).
Viverra civettina[e]	Malabar civet	India (Western Ghats)	CR	This species is possibly extinct because there are no recent reliable records since 1989 despite surveys (including with camera-trapping) in potentially suitable habitats. In any case, population size does not exceed 250 mature individuals (Mudappa *et al.*, 2016).

(*Continued*)

Table 1.2 (Continued)

Family and scientific name[a]	Common name	Distribution	*IUCN Red List* categorization	Main threats/concerns (Asssessors/reference)
Viverra megaspila	Large-spotted civet	Cambodia, China (?)[f], Lao, Malaysia, Myanmar, Thailand, Vietnam (?)[f]	EN	Past and projected dramatic population decline (> 50%) over the previous/next 15 years due to the combined effects of trade-driven overexploitation and habitat destruction/fragmentation. Species living almost exclusively in level lowland which is sought for conversion to agriculture, infrastructure, and settlement (Timmins *et al*., 2016b).

Population trends are deemed decreasing for all species, except for the population of the Iberian lynx, which is increasing. Island endemics are indicated with an asterisk.
[a] When relevant, alternative taxonomic treatments are provided in Appendix A.
[b] Molecular studies of Veron & Goodman (2018) have suggested that *Eupleres major* does not differ from *E. goudotii* (eastern falanouc), but additional studies are needed to confirm this.
[c] Veron *et al*. (2017) have now shown that Grandidier's vontsira should be considered a subspecies of broad-striped vontsira, namely *Galidictis fasciata grandidieri*, and that therefore the conservation status of the latter species should be reassessed.
[d] Treated as a separate species from *Procyon lotor* based on morphometric and genetic differences (McFadden *et al*., 2008; McFadden & Meiri, 2013). However, a reanalysis of the genetic data currently available suggests that the pygmy raccoon should be treated as a synonym of *Procyon lotor hernandezii* (Wagler, 1831), and, therefore, its conservation status may have to be revised (Louppe *et al*., 2020b).
[e] Nandini & Mudappa (2010) argued that *Viverra civettina* is possibly the same species as *V. megaspila* following transport of individuals to the Western Ghats (southern India).
[f] This species is regarded as Possibly Extinct in China and Vietnam (Timmins *et al*., 2016).

transported and introduced purposefully or involuntarily by humans have also brought about a series of challenges for indigenous small carnivores, leading to population size reductions attributable to the negative effects of alien predators, competitors, and pathogens, and this particularly on islands (Cuarón *et al*., 2004; Farris *et al*., 2017; Rasambainarivo *et al*., 2017). The burgeoning human population and wildlife trade in Asia – for meat, medicinal use of body parts and the pet industry – is of particular concern (Siriwat & Nijman, 2018; Nijman *et al*., 2019; Willcox, 2020). The potential effects of human-driven climate change on small carnivores are difficult to predict with accuracy. Some species are likely to be affected more severely than others, notably those living on islands (Struebig *et al*., 2015), but climate change may also lead to an increase in the distribution range of several species (Pandey & Papes, 2018). For example, projections based on ecological niche modelling suggest that introduced and invasive species such as northern raccoon and small Indian mongoose will expand their geographic range, and that by 2050, they will have an increasing influence on ecosystems and biodiversity, particularly in Europe (Louppe *et al*., 2019, 2020a). More generally, small carnivores may not be directly affected by climate change *per se*, but could theoretically be impacted by a change (reduction or increase) in the abundance of food resources.

The anthropogenic threats listed above are not exclusive to Endangered and Critically Endangered species as they affect and negatively impact Vulnerable, Near Threatened, and Least Concern species as well; hence, the need for at least a periodical reassessment of the conservation status of each species. Figure 1.4 shows that small carnivores generally fare better than large carnivores when it comes to conservation status, with a lower percentage of species being categorized as Near Threatened or threatened *sensu lato*. However, because small carnivore species richness is nine times higher than that of large carnivores, a much larger number of small carnivore species are threatened worldwide. The potentially grave ecosystem-wide implications of the extirpation of large carnivores across the globe are raised later in this chapter.

As discussed above, the apparent increase in the number of small carnivore species worldwide is primarily related to recent species splitting and proposals to elevate some subspecies to species level. While some (suggested) changes were grounded on a solid combination of morphological, molecular, and biogeographic data, other cases relied singly on phenotypic variations or single molecular-marker (often mitochondrial DNA) analyses. The latter, in combination with the recent use of the phylogenetic species concept based on diagnosability, has led to what some call an unwarranted 'species inflation', with some serious conservation implications (see e.g. Zachos *et al.*, 2013). While the term 'species' is generally regarded by governments and most funding bodies as the appropriate taxonomic unit when it comes to conservation, both taxonomic inflation and inertia have benefits and drawbacks (Zachos, 2013; Gippoliti *et al.*, 2018). It is likely that structured and concerted team efforts, such as that demonstrated by the IUCN SSC Cat Specialist Group to revise the taxonomy of the Felidae (Kitchener *et al.*, 2017), would ensure an accurate evaluation of the contentious cases. Periodical literature reviews or reassessments of the taxonomy and systematics/phylogeny of carnivore subgroups are also particularly encouraged (see e.g. Veron, 2010; Helgen *et al.*, 2013; Sato, 2016; Zrzavý *et al.*, 2018; Alvares *et al.*, 2019; Sato & Wolsan, Chapter 2, this volume; Veron *et al.*, Chapter 3, this volume), especially considering the fast pace at which the field of molecular biology is developing. Irrespective of their taxonomic rank, genetic lineages of high conservation priority (either already or yet to be identified) should receive full attention from governments and conservation organizations (Thakur *et al.*, 2018). For the sake of conservation, informed scientists should make it a responsibility to educate the designated authorities about the logic underlying their recommendations. In view of the evolving nature of biological lineages, 'species' or 'subspecies' are somewhat arbitrary terms used to describe unique biological entities (i.e. taxa) that share distinct, transmissible biological characteristics. Considering that recent reference works recognize the existence of between 990 (Wilson & Mittermeier, 2009) and 1233 (Wozencraft, 2005) subspecies of terrestrial carnivores, prioritizing may be called for irrespective of whether a focal taxon is called a 'species' or 'subspecies'. For example, Wilting *et al.* (2016) have convincingly demonstrated the conservation significance of the Javan leopard, *Panthera pardus melas*, subspecies for which only a few hundred individuals still live in the wild. When relevant, zoologists and conservationists should work hand in hand to define Evolutionary Significant Units (Ryder, 1986) as well as Management Units (Moritz, 1994), as notably proposed for the Andean cat, *Leopardus jacobita* (Cossíos *et al.*, 2012), and the Pampas cat, *Leopardus colocola* (da Silva Santos *et al.*, 2018). Conservation actions would then have to be prioritized based on the threat level pertaining to those 'operational units' under the species level.

Ecological Roles of Carnivores

Large carnivores such as lions, tigers, brown bears or grey wolves, *Canis lupus*, or brown bears, have drawn considerable attention from researchers. This is firstly due to their charisma, as indeed humans have long been fascinated by these magnificent creatures. Secondly, emphasis on research effort is a result of the potential of these species to be involved in human–wildlife conflicts (e.g. Rajaratnam *et al.*, 2016; Penteriani *et al.*, 2017; Moreira-Arce *et al.*, 2018; Kelly *et al.*, 2019; Ugarte *et al.*, 2019; Reyna-Saenz *et al.*, 2020) and the ensuing persecution and threats to several species and/or local populations (e.g. Bauer *et al.*, 2015; Jacobson *et al.*, 2016; Trinkel & Angelici, 2016; Durant *et al.*, 2017). Recovery of large carnivore populations and co-existence with humans, however, are not impossible, as exemplified by the current situation in Europe with grey wolves and brown bears (Chapron *et al.*, 2014). Reintroductions and rewilding may also assist in this context (Hayward & Somers, 2009; Wolf & Ripple, 2018; Linnel & Jackson, 2019; but see Alston *et al.*, 2019). Certainly, large carnivores and the 'landscape of fear' they create are vital for the regulation of land and aquatic ecosystems through cascading interactions across trophic levels. This has been dealt with in great depth in a large body of empirical and theoretical literature spanning two decades (e.g. Wright *et al.*, 1994; Palomares *et al.*, 1995; Terborgh *et al.*, 1999; Ripple &

Beschta, 2004; Ray *et al.*, 2005; Johnson *et al.*, 2007; Ripple *et al.*, 2014; Suraci *et al.*, 2016; Leempoel *et al.*, 2019; Hoeks *et al.*, 2020). Recent studies have shown that the presence of top carnivores constrains the distribution and/or abundance of mesocarnivores (Newsome *et al.*, 2017; Davis *et al.*, 2019; Jiménez *et al.*, 2019; Prugh & Sivy, 2020). On the other hand, apex carnivores may facilitate resource partitioning through the provision of carrion to smaller carnivores (Sivy *et al.*, 2018; Ruprecht *et al.*, 2021; cf. Prugh & Sivy, 2020) and facilitate overall species coexistence in both natural and altered ecosystems (Wallach *et al.*, 2015b). Equally, there is strong mathematical support showing that top predators *sensu lato* may induce the evolutionary diversification of intermediate-size predator species (Zu *et al.*, 2015).

Small carnivores, although represented worldwide by many more species, are often mistakenly thought to exert a weaker ecological influence at the ecosystem level. Although they do not impact on the same spectrum of prey as large carnivores, they are similarly important ecosystem regulators through structuring invertebrate and/or small mammal communities, including in rural agro-ecosystems (e.g. Williams *et al.*, 2018), which, in turn, may affect both lower and higher trophic levels (Roemer *et al.*, 2009). They may also be important in seed dispersal (e.g. Koike *et al.*, 2008; López-Bao & González-Varo, 2011; see review in Nakashima & Do Linh San, Chapter 18, this volume), which may both enhance forest regeneration and plant gene flow (Jordano *et al.*, 2007), thus reducing inbreeding depression. The roles of small carnivores in shaping ecosystems have also been shown through accidental introductions, which have been numerous for this group of predators (Boitani, 2001; Gantchoff *et al.*, Chapter 20, this volume). Finally, where large carnivores have been extirpated by humans – directly by persecution or through habitat modifications – small carnivores have or may become dominant predators in these ecosystems. This may alter their abundance, ecological roles, and importance in the corresponding food webs, and sometimes destabilize communities, drive local extinctions, and reduce overall biodiversity (e.g. Trewby *et al.*, 2008; Prugh *et al.*, 2009; Colman *et al.*, 2014; Wallach *et al.*, 2015a; Alston *et al.*, 2019; Cove & O'Connell, Chapter 21, this volume).

Research Efforts on Carnivores

Although small carnivores have been the focus of numerous research projects over the past several decades, smaller species have not received the same attention as that bestowed upon large carnivores. In addition, there is a huge disparity in the research efforts directed toward small carnivores, with some species intensively studied and others superficially or not at all. Brooke *et al.* (2014) reviewed 16 367 peer-reviewed papers focusing on at least one of the 286 species of the order Carnivora (including pinnipeds; Wozencraft, 2005) published from 1900 to the end of 2010. Unsurprisingly, they found that the most charismatic families of terrestrial carnivores were over-represented in the literature; namely Canidae (3387 publications), Felidae (2968), Ursidae (2002), and Hyaenidae (319), the sum of which corresponds to exactly two-thirds of all papers published on terrestrial carnivores. When the number of species per family was taken into account, the ranking remained relatively unchanged, with the Ursidae topping the list (with an average of 250 papers per species), followed by the Canidae (97), Hyaenidae (80), and Felidae (74). By comparison, the best-studied family of (mostly) small carnivores, the Mustelidae, was the subject of an impressive 2968 papers, but this corresponds to an average of only 49 papers per species. However, the above values are somewhat misleading because the distribution of papers within families is further biased toward the large species. Among the Felidae, for example, 52% of the papers focused on the 7 large felids, while the remaining 48% were dedicated to the 33 species of small felids (Z. Brooke, personal communication). Comparable trends were observed for the Canidae, with the notable exception of the 'small' red fox, which generated an imposing 923 publications. Similarly, among the Mustelidae, 4 species accounted for 46% of all publications for this family (rich of at least an additional 55 species); these are the European badger (517 papers), Eurasian otter (369), European polecat (233), and stoat (228). Research emphasis seems to be attributable to a series of additive factors: large distributional range, initial higher research effort by European zoologists, lack of larger carnivores (notably in the UK and Ireland, where natural history studies have always played a preponderant role), the implication of some

species in major zoonoses (rabies, bovine tuberculosis, and sarcoptic mange), and introductions to non-native environments leading to undesirable effects on native wildlife. Other species-rich families such as the Herpestidae and Viverridae averaged only 10 and 6 papers per species, respectively. Similarly, low average numbers of papers were obtained for the Mephitidae (18) and Eupleridae (5). Strikingly, there were no records of publications on 28 small carnivore species from 7 families, including 9 mongoose, 6 mustelid, and 5 viverrid species. Among Herpestidae, group-living species such as meerkats, *Suricata suricatta*, and banded mongooses, *Mungos mungo*, have attracted most of the attention, as they have been used as model species to understand the evolution of sociality. Of course, this literature survey would not have picked up 'grey literature' (e.g. technical reports or unpublished academic theses), papers published in small regional journals, or those written in languages other than English. Overall, however, the results clearly confirmed the suspicion that, until the end of 2010, there was a massive disparity in the research efforts on large vs. small carnivore species globally.

Considering the relatively recent and in-depth bibliometric studies of Brooke *et al.* (2014), and the broad but general scope of this introduction, we did not aim to undertake a detailed analysis of the evolution of the number of papers published over the last decade on each of the > 232 species of the world's small carnivores. Rather, we sought to understand whether the situation had improved. To that end, two literature datasets that we retrieved and analyzed provide some interesting insights.

We first ran a search for all the publications containing a combination of keywords referring to small carnivores (see details in Figure 1.5 caption) as a topic using all databases accessible in Web of Science (Clarivate Analytics). The output list was then imported into EndNote X7.8 (Thomson Reuters) and curated, after which all papers that did not focus on carnivoran, terrestrial predators were discarded. This exercise yielded a total of 618 articles published

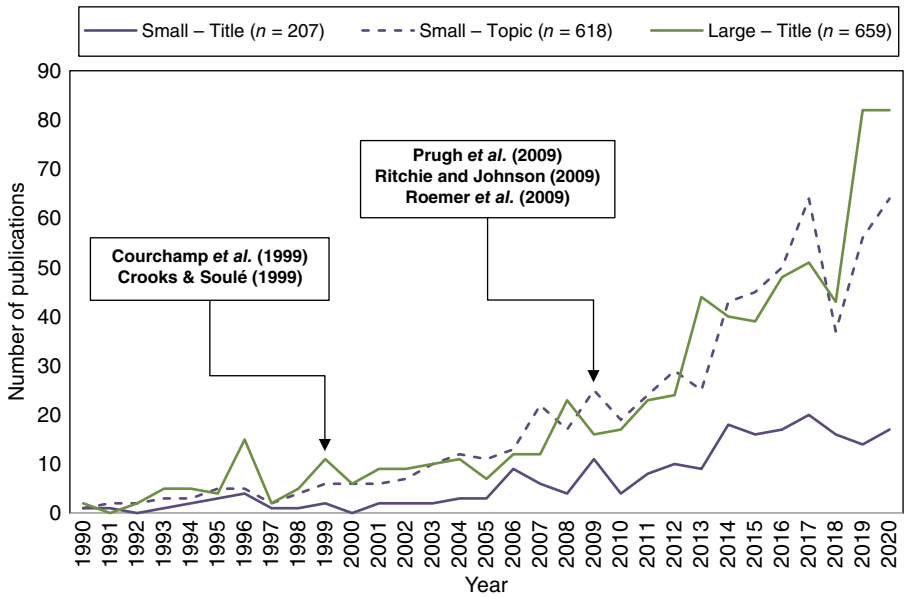


Figure 1.5 Number of scientific publications from 1990 to 2020, as retrieved from the Web of Science database (https://apps.webofknowledge.com). The purple continuous line corresponds to the number (*n*) of publications with the terms 'small carnivores', 'mesocarnivores', 'mesopredators' or 'mid-size(d)/medium-size(d) carnivore(s)/predator(s)' included in the title. The purple dashed line represents all publications with the same keywords as a topic. The green continuous line depicts publications with the terms 'large/top/apex carnivore(s)/predator(s)' in the title. Datasets were curated to only include publications on terrestrial members of the order Carnivora. The years of publication of five seminal papers or reviews on the roles of mesopredators are also indicated in the graph.

between 1990 and 2020. Providing that this subsample is representative of the trends that would have been observed had all publications been searched for (i.e. with the >232 species scientific and English names used as keywords) and curated, Figure 1.5 suggests that the number of publications on small carnivores has increased in a nearly exponential fashion since 1990, with a significant increase only taking place from 2009 onward. During that year, three seminal review papers were published: one focusing on the ecological role of mesocarnivores (Roemer *et al.*, 2009); another on the rise of mesopredators in ecosystems where apex predators have been extirpated (Prugh *et al.*, 2009) – a phenomenon known as 'mesopredator release' (Soulé *et al.*, 1988; Litvaitis & Villafuerte, 1996; Courchamp *et al.*, 1999; Jachowski *et al.*, 2020); and a third arguing that effective biodiversity conservation requires proper knowledge of predator interactions and understanding of the mechanisms underlying mesopredator release (Ritchie & Johnson, 2009). There is no doubt that these now well-cited publications have highlighted the roles and importance of the smaller carnivores, thereby boosting research effort on them.

In a second step, to infer whether the research efforts were focusing on small carnivores as research models rather than on species *per se*, we restricted the above dataset to publications that included any of the selected keywords in the title. This reduced the total to 207 articles. As apparent in Figure 1.5, the number of publications meeting this new criterion increased over the past decade, but not as sharply as the overall number of publications whose main topic was small carnivores. This difference may indicate that although small carnivores are receiving more attention from the scientific community as model organisms (for example, to test the mesopredator release theory), there might also be an increased focus on the general biology, ecology, and conservation of these fascinating organisms. This discrepancy in numbers seems to be accounted for by the current boom in camera-trapping studies worldwide (Rich *et al.*, 2017), accompanied by an exponential increase in publications (Rovero & Zimmerman, 2016) which have provided insights into the distribution, relative abundance, activity patterns, and interspecific relationships of numerous mammalian species.

As a third and last step in evaluating how small carnivore research fared in comparison with that on the larger species, we searched for all the publications containing a combination of keywords referring to large carnivores in the title of the article (see details in Figure 1.5 caption). This new search yielded a total of 659 curated articles published between 1990 and 2020. The same search with the selected keywords as topic yielded over 83 000 non-curated references. While a large number of those seemed to be unrelated to our target keywords, it is clear that several thousands of papers focusing on large carnivores have been published over the last 10 years. These literature searches strongly suggest that research on carnivores is still disproportionately geared toward the larger species. While it is possible that the observed increase in small carnivore research is partly or even largely due to (and therefore proportional to) an overall increase in the research efforts and scientific publications over the past decade, it is reassuring to see that small carnivores have at least been included in this trend. Whatever the reason(s) behind the nearly exponential increase in the number of publications, it signifies an increase in both our interest and scientific knowledge of small carnivores.

A preliminary examination on the major institutions driving the research and the regions where small carnivore research is taking place reveals that research efforts are not equally distributed. About one-third of the research is carried out in North or Central America, East Africa, and Southeast Asia by teams led by North American scientists. An equal amount of research output is produced by European researchers (UK/Ireland, Spain, France, Germany, Portugal, Italy, and Scandinavia), working in Europe, as well as in North and Equatorial Africa, Arabia, and Southeast Asia. The last third of publications emanate from Australia, South Africa, Brazil, India, China, and the rest of the world, with research generally taking place in the home country of the researchers with the exception of some Japanese researchers working in Equatorial Africa and Borneo.

The general trends depicted above seem to be only partly reflected in the geographic coverage of articles and notes published in *Small Carnivore Conservation* (SCC), the scientific journal of the IUCN SSC Small Carnivore Specialist Group. Indeed, 41% of papers

published until March 2017 in SCC comfortingly focused on Asian small carnivore species (González-Maya & Ramírez-Chaves, 2017). In contrast, other continents have been largely under-represented, with only 13% and 11% of publications dealing with African and American species, respectively (cf. continental proportions of small carnivore species in Figure 1.2). To remedy this unbalance in coverage, however, SCC has recently encouraged and promoted research in the Americas (and particularly in South and Central America; Schipper *et al*., 2009) and in Africa (Do Linh San & Somers, 2013) through the production of dedicated Special Issues. Currently, the majority of publications in SCC report on faunal surveys, new range records, and unusual behaviours. Often these reports arise as by-products of research projects focusing on other animal taxa.

For all of the reasons listed above, it now appears that the tide is changing with regards to prioritizing small carnivore studies. We hope to see more small carnivore-dedicated work in the future, particularly where species richness and diversity are high and where knowledge gaps are apparent. In particular, research on threatened and Data Deficient species (*sensu* IUCN, 2021) is of critical importance.

Purpose and Structure of the Book

This book aims at filling a gap in the scientific literature by elucidating the important roles of the world's small carnivores and documenting the latest knowledge acquired on them. Specifically, our plan was to bring together contributions dealing with several aspects of small carnivore evolution, ecology, behaviour, and conservation biology. While several recent books have focused on restricted taxa of small carnivores (Harrison *et al*., 2004; Santos-Reis *et al*., 2006; Aubry *et al*., 2012; Proulx & Do Linh San, 2016; Zalewski *et al*., 2017), this volume deals with a wide range of species belonging to numerous families. The species of interest predominantly include badgers, martens, otters and allies (Mustelidae), civets, genets and allies (Viverridae), mongooses (Herpestidae), raccoons (Procyonidae), and skunks (Mephitidae). Other taxa, i.e. the smaller representatives of the Canidae and Felidae families, are well represented in whole-taxocenosis studies, meta-analyses and reviews; several of these species have also been covered comprehensively in books edited by Macdonald & Sillero-Zubiri (2004) and Macdonald & Loveridge (2010), respectively. A recent addition to this series – published during the preparation of this book – deals with several aspects of the biology and conservation of musteloids (Macdonald *et al*., 2017). This is encouraging and further indicates that small carnivores are progressively enjoying the research attention they deserve.

While a wide range of methods are described and used by the numerous authors of this edited book, no section is specifically dedicated to research techniques. Readers seeking greater details, including more technical information on the methods currently used in carnivore research and more broadly in animal ecology, are encouraged to consult books dedicated to these topics, i.e. edited works by Boitani & Fuller (2000), Long *et al*. (2008), O'Connell *et al*. (2011), Boitani & Powell (2012), Silvy (2012a,b), Meek *et al*. (2014), and Rovero & Zimmerman (2016). The books edited by Gittleman (1989, 1996), Gittleman *et al*. (2001), and Goswami & Friscia (2010) also provide complementary information on several aspects of carnivore behaviour, ecology, evolution, and conservation.

The present volume contains a series of broad reviews (nine chapters) on systematics, biogeography, ecomorphology, ecology, and conservation issues, including some meta-analyses. However, due to the paucity of data available for several disciplines, comprehensive reviews of all topics were not always possible. Instead, some contributors were invited to write chapters summarizing their research work on the autecology, interspecific interactions, and/or conservation of selected small carnivore species (three chapters). Finally, as mentioned above, the field of small carnivore research is just stepping out of its infancy and, thus, the future will continue to be one of fundamental research. Hence, the book also contains 10 original research papers that will bring new insights into a wide range of disciplines, including morphological studies, movement ecology, disease dynamics, and interspecific interactions.

Following the present **introductory chapter (Part I)**, the core of the book is divided into four main parts. Contributions were allocated to one of four sections, even though some chapters deal with a broad

range of topics and could have been classified in any of two or even three sections. For example, ecological studies presented here often had important implications for management and conservation, especially those carried out in human-dominated, and hence, modified or degraded landscapes.

Part II consists of five chapters focusing on **evolution**, **systematics**, **and distribution**. These topics are in themselves important in terms of general biology and often carry implications for the conservation of biodiversity. Recent molecular phylogenetic approaches have overwritten the traditional taxonomy based on phenotypic characters (e.g. morphology) and have detected many homoplasious convergent evolutions (Springer *et al*., 2004). Resolving the taxonomic issue and setting the unit are required as a premise in the field of conservation biology (Frankham *et al*., 2010). Molecular data have also greatly improved our understanding of how the clade genesis is correlated with the Earth's environmental changes (Condamine *et al*., 2013) or how indices for conservation prioritization could be obtained (e.g. EDGE; Isaac *et al*., 2007).

The first two chapters of this section deal with taxonomic, evolutionary, and conservation issues by focusing on molecular phylogenetics. In Chapter 2, Jun J. Sato and Mieczyslaw Wolsan review the molecular phylogenetic studies on the long-standing evolutionary puzzle presented by the taxonomic position of the red panda and describe the promising approaches that have reliably elucidated caniform carnivoran phylogeny. They further provide an up-to-date subfamily classification of the family Mustelidae (weasels, martens, otters, badgers, and allies; Caniformia), and show a correlation between lineage diversification and global climatic change. Their review also suggests that the priority for species conservation should be inferred from the supermatrix-based phylogenetic tree instead of the supertree that has commonly been used. In Chapter 3, Géraldine Veron, Marie-Lilith Patou, and Andrew P. Jennings review the molecular systematics of the family Herpestidae (mongooses and allies; Feliformia) as well as the Malagasy 'mongooses' currently classified into Eupleridae, and provide a novel taxonomic framework especially for the Asian mongooses (the genus *Urva*) based on a reliable molecular phylogeny. Using this phylogeny, they also discuss the evolution of life-history traits such as sociality within this family and conclude that the evolution of sociality occurred once during the Late Miocene to Pliocene in Africa, with more open habitats likely favouring group living.

The following chapters adopt rapidly developing statistical approaches, species distribution modelling (SDM; Svenning *et al*., 2011), ecomorphology (Werdelin & Wesley-Hunt, 2010), and/or ecometrics (Polly *et al*., 2011) analyses, combined with environmental variables available in the WorldClim database (Hijmans *et al*., 2005). These methodologies are useful to assess the evolutionary responses (e.g. adaptation) to the biotic and/or abiotic environmental changes. In particular, adaptation should be considered in defining how to conserve populations or species (Funk *et al*., 2012). In Chapter 4, Robert S. Sommer and Jennifer J. Crees review the subfossil evidence of the past distributional history of small carnivores in Europe during the Late Pleistocene, and discuss how climatic changes and human activity influenced their distribution. They propose species-specific refugia and post-glacial recolonization patterns for small carnivores in Europe. The inference of the past distribution based on SDM suggests that, in contrast to the case of large carnivores, small carnivores were resilient to human impacts during the Holocene. In Chapter 5, Carlo Meloro examines the ecomorphology of small carnivore assemblages in six independent terrestrial ecosystems and shows that tropical guilds in Gunun Lensang, La Amistad, and Yasuni assemblages possess a higher diversity in mandible shape, while guilds in higher latitudes (Krokonose, Kruger, and Yellowstone) exhibit a shortage of some parts in the mandible morphospace. His ecometrics analysis also shows that the amount of lagomorphs and precipitation in the focal study sites are correlated with a higher morphological disparity, hence highlighting the likely importance of biotic and abiotic environmental changes on the historical community assembly of small carnivore guilds. In Chapter 6, Adam W. Ferguson, Richard E. Strauss and Robert C. Dowler investigate coat-colour variations in the North American hog-nosed skunk, *Conepatus leuconotus*. They present a novel statistical technique to assess quantitative morphological variations and clarify that the amount of the dorsal whiteness in this skunk species is larger in individuals living in open and dry habitats in northwestern parts of the

distribution range (Arizona, Colorado, New Mexico, and northern Mexico), while individuals with less dorsal whiteness (or more blackness) are restricted to lower latitude areas, namely the Gulf of Mexico and Central America. Their statistical ecometrics analyses suggest that canopy cover, ground surface moisture, and/or ambient temperature might explain the observed coat-colour variations. Their results are consistent with the intermediate aposematism hypothesis, which posits that there is a selective balance between conspicuousness and crypsis in aposematic animals.

Part III comprises six chapters focusing on **ecology**, **behaviour, and – peripherally – diseases** through contributions that are largely based on or derived from data collected in the field. As alluded previously, basic natural history data are still missing for a majority of small carnivore species, thus, field studies are paramount. In addition to providing baseline biological and ecological information, field studies contribute empirical data to laboratory and computer (modelling) analyses.

A large number of mammals (see review table in Dröscher & Kappeler, 2014), including carnivores, use latrines which are believed to play an important role in olfactory communication. In Chapter 7, Christina D. Buesching and Neil R. Jordan review the available literature and show that detailed knowledge of specific information exchange is still lacking for most carnivores. They present an innovative and well-thought-out research framework to test hypotheses about the function of latrines in carnivores and other species. Relying on their extensive field experience, they then review current knowledge on latrine use in three small carnivore species and test some of the hypotheses put forward to explain the function(s) of latrines. The authors highlight that a combined approach (namely spatial, temporal, individual-based, and signal-content-related) is needed to clarify the function(s) of latrines in different species.

In the UK and Ireland, the European badger makes extensive use of latrines. This species is also a known reservoir and vector of bovine tuberculosis (Gallagher & Clifton-Hadley, 2000). Bovine tuberculosis is an infectious disease that not only causes animal health issues but also economic and logistical hardship to livestock farmers (McCulloch & Reiss, 2017). Extensive knowledge of badger ecology and behaviour is therefore vital in this context. In Chapter 8, Andrew W. Byrne, James O'Keeffe, and S. Wayne Martin study the movement patterns of European badgers in Ireland based on an extensive mark–recapture dataset collected at a large spatial scale. Their analytical models suggest that density-dependent mechanisms affect badger movement patterns within subpopulations. Movements are generally shorter and less frequent in higher-density than lower-density areas. However, there was no net tendency for badgers to move into higher- or lower-density subpopulations. The authors discuss the implications of these findings for understanding the dynamics of bovine tuberculosis across badger populations in rural areas.

Human activities taking place in agricultural landscapes globally are expected to have some direct and indirect effects on a majority of organisms. In Chapter 9, Diego F. Castillo and Mauro Lucherini investigate the behavioural adaptations of Molina's hog-nosed skunk, *Conepatus chinga*, to human-modified landscapes in Argentina. These authors found considerable behavioural plasticity by skunks that facilitated the species' persistence in their agricultural study site, but conclude that the loss of grasslands through conversion to agricultural land is likely decreasing skunk abundance across the Pampas.

In extreme cases, some highly adaptive small carnivore species have been able to successfully colonize urban areas thanks in part to their eclectic diet (for a recent review, see Gehrt *et al*., 2010). Due to the high abundance of certain food resources in urban areas, some species may reach higher densities than in their natural habitats, hence becoming synurbic, *sensu* Francis & Chadwick (2012). In Chapter 10, Jan Herr and Timothy J. Roper used radio-telemetry to investigate the activity rhythms of the stone marten, *Martes foina*, in urban areas, and question whether these may be affected by anthropogenic factors. Interestingly, their results strongly suggest that behavioural adaptation in urbanized habitats occurs primarily by temporal avoidance, rather than by tolerance, of human activity.

Other small carnivore species such as the European mink, *Mustela lutreola*, which is listed as Critically Endangered by IUCN (2021), may face more challenging scenarios especially when infectious diseases are among their mortality factors. In Chapter 11, Christine

Fournier-Chambrillon and several co-workers monitored a mink population over nine years in Navarre (Spain) and recorded a population crash concordant with a canine distemper virus outbreak. The population seems to have recovered slowly, but the authors advocate that strong conservation measures for this and all other relictual nuclei populations of the western European mink are urgently needed.

As noted previously, camera-trapping is now a widespread and effective sampling technique in wildlife research (McCallum, 2012; Wearn & Glover-Kapfer, 2019). However, the use of camera-traps requires proper planning and survey design (Ancrenaz *et al*., 2012; Wearn & Glover-Kapfer, 2017; Kays *et al*., 2020). Camera-traps are attractive because they allow researchers to detect or confirm the presence of species in targeted areas and determine species richness, diversity, and community structure (Ahumada *et al*., 2011; several chapters in Meek *et al*., 2014). They also allow to obtain abundance and density estimates (Carbone *et al*., 2001; Nakashima *et al*., 2017), although some concerns were raised about the accuracy of such estimates when the field study design violates key assumptions (Foster & Harmsen, 2012; Sollmann *et al*., 2013; Tobler & Powell, 2013; Rogan *et al*., 2019). The use of camera traps also enable to gather preliminary information on activity patterns of target species (Rowcliffe *et al*., 2014; Frey *et al*., 2017; Botts *et al*., 2020) and evaluate their spatial occupancy, distribution, habitat use and daily movements and ranges (e.g. several chapters in O'Connell *et al*., 2011; Allen *et al*., 2018; Dechner *et al*., 2018; Palencia *et al*., 2019). Lastly, two- or multi-species occupancy models and temporal overlap analyses allow to infer competition or coexistence (Gerber *et al*., 2012; Haidir *et al*., 2018; Li *et al*., 2019; Santos *et al*., 2019; Mills *et al*., 2019), as well as predator–prey and other interactions (Cusack *et al*., 2016; Pudyatmoko, 2019; Dias *et al*., 2019; Vilella *et al*., 2020). This technique is particularly applicable to understudied species that are relatively small, nocturnal, elusive, and/or live in dense cover. For example, little is known of the ecology of the African civet, *Civettictis civetta*, including its abundance and density in different habitat types. Lisa Isaacs, Michael J. Somers, and Lourens H. Swanepoel (Chapter 12) provide the first density estimates of the largest African viverrid across a landscape gradient, with densities reaching as high as 13 individuals/km^2. The authors highlight the value of using 'by-catch' (camera-trap) data obtained during non-invasive surveys of large charismatic species for understanding aspects of small carnivore ecology. More importantly, they emphasize the need to understand small carnivore abundances and the factors that influence them, in particular, guild-level effects and the role of anthropogenic drivers.

Part IV contains seven chapters that focus on **interspecific interactions and community ecology in relation to management and conservation**. In Chapter 13, Zach J. Farris and his colleagues used camera-trapping and a new spatio-temporal technique to demonstrate that the spotted fanaloka, *Fossa fossana*, a native and Vulnerable (*sensu* IUCN, 2021) Malagasy carnivore, is likely excluded from degraded forests by the introduced small Indian civet, *Viverricula indica*. The authors propose management options and correctly highlight that their novel analytical approach has wide-ranging applications for conservation managers working to address the negative impacts of introduced species on indigenous wildlife. Luigi Remonti, Aritz Ruiz-González, and Alessandro Balestrieri (Chapter 14) similarly explore the effects of interspecific competition and habitat constraints on species' distribution ranges and abundance, here focusing on two indigenous nocturnal small carnivores in northern Italy. Using a wide range of methods, these authors convincingly demonstrate that the pine marten, *Martes martes*, which is normally associated with mature coniferous and mixed forests, has experienced a southward range expansion reaching the intensively cultivated Po-Venetian Plain. Colonization took place by using the best-conserved riparian forests as corridors; further expansion southward is constrained only by the River Po. Genetic analyses revealed that this expansion was concomitant with a range contraction of the similar-sized stone marten, probably due to interspecific food competition, as inferred from dietary analyses.

Competition among small carnivores may also take place in space and time. Using remote-camera surveys, Yoshihiro Nakashima and co-workers (Chapter 15) show that most pairs of small carnivores in Moukalaba–Doudou National Park (Gabon) differ in either habitat use or time of activity, which may

promote their coexistence in the rainforest across this region. They propose that the relative proportion of small carnivores over space and time likely reflects the degree of degradation of the forest. Hence, maintenance of habitat heterogeneity may be important for the conservation of these species. A long-term camera-trapping programme should prove a very useful monitoring tool. In Chapter 16, Aaron M. Haines, Lon I. Grassman Jr, and Michael E. Tewes explore niche separation through resource partitioning in a carnivore community in north-central Thailand. Using radio-telemetry data, they investigated spatial overlap between individuals from six sympatric carnivore species and correlate this overlap with variables reflecting differences in morphology, habitat use, and activity patterns. Results show that species with greater differences in carnassial tooth length tend to avoid each other spatially, whereas species that exhibit different activity patterns in closed habitat cover display a higher spatial overlap. The study therefore suggests that smaller-toothed carnivores may try to avoid antagonistic confrontations with larger-toothed carnivores. Interspecific competitive killing and intraguild predation (involving prey consumption) are believed to be important factors shaping the spatio-temporal distribution of species in carnivore communities (Palomares & Caro, 1999; Donadio & Buskirk, 2006). With this context in mind, Colleen M. Begg and colleagues (Chapter 17) examined the interactions between honey badgers, *Mellivora capensis*, and other predators in the Kalahari semi-desert, South Africa. During nearly 6000 hours of monitoring and field observations of radio-tagged animals, the authors recorded antagonistic interactions between honey badgers and 12 other carnivore species. Intraguild predation (or attempted) was common, and honey badgers acted both as predators and prey. In addition, foraging associations between honey badgers and seven other predator species (two mammals, five birds) were recorded, mainly commensalist or producer–scrounger interactions with black-backed jackals, *Canis mesomelas*, and pale chanting goshawks, *Melierax canorus*. These fascinating results call for more observation-based research of interspecific interactions at the community-wide scale. Although labour-intensive and often physically demanding, observational studies constitute a much-needed complement to other field and laboratory techniques, and, in many cases, are the only method capable of obtaining specific information (e.g. detailed interspecific interactions).

As noted earlier, not all small carnivores are strictly carnivorous. Some species feed seasonally or exclusively on fruit rather than on animal matter. In Chapter 18, Yoshihiro Nakashima and Emmanuel Do Linh San review the published literature on frugivory and seed dispersal in small carnivores. The authors show that small carnivores play a crucial role as seed dispersers by transporting seeds beyond the crown of the mother plant and subsequently defecating viable seeds. While faeces (and seeds) are often deposited in areas which may be unfavourable for plant growth, in fragmented landscapes, frugivory coupled with long-distance seed dispersal may promote vegetation recovery and enhance plant-genetic diversity.

The fourth section of the book closes with an extensive account by Andrew P. Jennings and Géraldine Veron (Chapter 19) who synthesize the results of their research work on the ecology and distribution of Southeast Asian civets and mongooses. The authors first report on the spatio-temporal ecology of Malay civets, *Viverra tangalunga*, and short-tailed mongooses, *Urva brachyura*, in Sulawesi and/or Peninsular Malaysia, as determined through radio-telemetry. They then report on the predicted distribution of 10 small carnivore species as estimated through ecological niche modelling. Lastly, they present data from their camera-trapping project on Sumatra, where they detected only three small carnivore species. The Malay civet seems to be the most affected by the extensive oil palm plantations. In their discussion, the authors suggest that forest-dependent civet and mongoose species may be threatened by human activities such as forest exploitation (leading to habitat loss, degradation, and fragmentation), hunting, and wildlife trade.

Exploring this topic, **Part V** consists of four chapters focusing on **interactions between small carnivores and people**, **as well as on conservation issues for small carnivores**, **their prey**, **and possible competitors**. In their review on carnivore reintroductions, Breitenmoser *et al*. (2001) listed 12 small carnivore species, including the endangered black-footed ferret, *Mustela nigripes*, which have been reintroduced in an attempt to re-establish populations within their

historical range. In other cases, translocations have been used to supplement threatened populations (see Bricker *et al*., Chapter 23, this volume). This contrasts with the numerous cases of introductions of non-native carnivore species, either domestic animals that have turned feral, animals that have escaped from captivity, animals which have been accidentally transported, or (most frequently) animals that were deliberately released (Boitani, 2001). In Chapter 20, Mariela G. Gantchoff, Nathan S. Libal, and Jerrold L. Belant summarized information on small carnivore introductions worldwide and assessed, irrespective of the cause of introduction, why some have succeeded, yet others failed. They identified 253 documented introduction events of 24 species from five families (out of the nine dealt with by the IUCN SSC Small Carnivore Specialist Group), and show that introduction success is dependent on the absence of congeners and preadaptation to the climatic conditions that prevail in the introduction area, a larger body size coupled with smaller litter size, and a carnivorous diet. Interestingly, the number of individuals introduced did not determine establishment success. As biological invasions become increasingly widespread (Seebens *et al*., 2018), understanding the biological and environmental factors affecting introduction success is important for conservation and management. Indeed, the numerous introductions of small carnivores worldwide sometimes resulted in adverse effects on threatened and endangered species. Michael V. Cove and Alan O'Connell (Chapter 21) highlight these issues and summarize the effects which have included population reductions and species extinctions, in some instances, with effects that cascade throughout the entire ecosystems. Improved methodologies to understand the relative effects of small carnivores on threatened species will help conservationists develop management strategies that target the primary drivers of species declines.

The importance of small carnivores to humans is dependent on diverse subsistence, social, cultural, economic, and religious values. Tim L. Hiller and Stephen M. Vantassel (Chapter 22) synthesize extensive and diverse literature to highlight the roles of these species in human societies. From early use as subsistence foods to current global marketing of species in the fur trade and concerns from overexploitation as bushmeat, use of small carnivores by humans is complex and widespread. Effective regulation of legal and illegal uses at national and international levels is necessary to ensure the conservation of many species. As an example, the distribution and abundance of North American river otter, *Lontra canadensis*, has been adversely affected by human persecution and habitat degradation. Through telephone and email surveys, Emily A. Bricker and her collaborators (Chapter 23) documented a remarkable recovery of this species, now occupying at least portions of its range in every US state and Canadian province but one, with stable or increasing populations. This recovery was due in part to expansions of extant populations augmented by numerous reintroductions. However, because of vulnerability to overharvest, the authors recommend that conservation strategies include effective harvest management and field monitoring of the species distribution and status to identify threats that may adversely affect their long-term recovery. In an addendum, a subset of the authors also express concern about the rationale for the extensive expansion in the trapping of river otters that has ensued completion of reintroduction projects.

The book closes with an **Appendix section (Part VI)**. For readers interested in particular species, Appendix A lists the 232 species of small carnivores considered by IUCN (2021) and informs on chapters in which each species is dealt with or mentioned in this book. The Appendix also provides alternative scientific and common names (when relevant), average body mass, global distribution, number of countries where species are native or have been introduced, as well as information on conservation status and population trends. More details on the biology, ecology, and conservation status of each species can be found in Wilson & Mittermeier (2009), Hunter & Barrett (2018), and IUCN (2021). Appendix B provides a list of the main small carnivoran taxa that have been the subject of discussions as to whether they should be attributed species or subspecies level. Although detailed, the list is likely not exhaustive considering the large number of subspecies of small carnivores described and considered to date.

In summary, this compendium presents contributions based on a wide range of techniques, which we suggest realistically reflect the state of our current

knowledge on the world's small carnivores. Further, it illustrates the varied forms of scientific outputs (reviews, meta-analyses, project syntheses, and original research papers) that current and future small carnivore researchers may be expected to encounter and produce throughout their careers. Many of the world's leading and upcoming small carnivore biologists contributed a chapter, and we hope that this book will become an important reference for all researchers, students, and wildlife professionals working on evolution (including genetics, phylogeography, taxonomy, and systematics), ecology, behaviour, and conservation of the world's small carnivores. Although this volume suggests that a substantial amount of knowledge has been accumulated on at least a subset of small carnivore species, the field of small carnivore science remains wide open. We therefore hope that this book will stimulate much-needed research globally and lead to exciting findings on these fascinating creatures. People working with large carnivores and mammals, in general, may also find this resource of value, as most of the widely tested or cutting-edge techniques described here can be successfully applied to other species.

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