Biological Conservation 255 (2021) 109005

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Review

Shining the spotlight on small mammalian carnivores: Global status and threats

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ARTICLE INFO

Keywords:
Assessment
Carnivore
IUCN red list
Large
Meso
Small

ABSTRACT

Small mammalian carnivores (Carnivora <16 kg) carry out important roles in ecosystems, such as influencing ecosystem structure and providing numerous ecosystem services. Despite their importance, there are contrasting views on the required conservation and management needs for species within this group. In a review of the IUCN Red List species-level assessments, we found that 53 small carnivore species were threatened (CR, EN, or VU) compared to 15 large. However, there were similar proportions of large (4%, 9%) and small (1%, 9%) carnivores endangered with extinction (CR or EN, respectively). We did not find support for small carnivores benefiting from mesopredator release in a global context; more than half of both large and small carnivore species decreasing, suggesting parallel declines. On average, large carnivores received their first IUCN assessment 10 years before small and, since their first assessment, small carnivores have received fewer assessments than large, highlighting the disparity in conservation attention within the guild. The leading threats for all carnivores include biological resource use and land use change. We review the major threats to threatened small carnivores and suggest areas for priority research and conservation. Collectively, we show that small carnivores are as endangered with extinction as are large carnivores, and that small carnivores should be of conservation concern globally, but particularly in species-rich regions of Southeast Asia, sub-Saharan Africa, and Madagascar. To inform conservation, we encourage more research into the basic ecology and demography of small carnivores, particularly regarding current and future threats in the face of global change.

1. Introduction

A great deal of conservation attention is focused on large carnivores, which often play important ecological roles in ecosystems. Large, terrestrial (i.e. living predominantly on land) mammalian carnivores have been extirpated or experienced declines in distribution or abundance in many regions globally (Ripple et al., 2014) and, given their typically large area requirements and popularity, often serve as flagship or umbrella species for conserving ecosystems (Ray et al., 2013). These species are typically apex carnivores in the systems they inhabit and can exhibit strong top-down direct and indirect effects on herbivores (Ripple and Beschta, 2012; Le Roux et al., 2019) and subordinate carnivores (Ritchie and Johnson, 2009). Previously, some have claimed that subordinate, smaller carnivores have benefited from the loss of larger carnivores, to the extent that rapid expansion and growth of smaller carnivore populations globally has been detrimental to ecosystem function and has had high economic and social costs (Prugh et al., 2009; Ritchie and Johnson, 2009; Brashares et al., 2010).

While some smaller, non-apex carnivores (hereafter referred to as small carnivores) have expanded their range over the past century (Arnold et al., 2012; Hody and Kays, 2018), the extent to which small carnivore species have benefited from 'release' from large carnivore predation and competition is highly context-dependent and known to be limited to only a few species (Allen et al., 2017; Haswell et al., 2017; Jachowski et al., 2020). Further, there have been calls for the conservation of small carnivores on several continents (Belant et al., 2009; Do Linh San et al., 2013; Proulx, 2020). In 2009, 62% of small carnivore species in the Americas had declining populations (Belant et al., 2009). In mainland Africa, Do Linh San et al. (2013) estimated that 27% of small carnivore species had decreasing population trends, and almost half of all species' population trends were unknown – highlighting the need for further conservation assessments. Moreover, since 2015,

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https://doi.org/10.1016/j.biocon.2021.109005
Received 28 July 2020; Received in revised form 20 January 2021; Accepted 24 January 2021

although six were down listed, 19 small carnivores were up listed to a higher IUCN category (González-Maya, 2018). Thus, there are contrasting views on the status and conservation need of small carnivores where, within this group, some are cited as needing conservation (e.g. Ethiopian wolves *Canis simensis* (Ash, 2001), Andean cats *Leopardus jacobita* (Cossíos et al., 2012), black-footed ferrets *Mustela nigripes* (Jachowski and Lockhart, 2009)) and others as needing control (e.g. coyotes *Canis latrans* (LeSher, 2020), golden jackals *Canis aureus* (Raichev et al., 2013), stoats *M. erminea* and least weasels *M. nivalis* (Mcdonald and Harris, 2002)), at both regional and global scales.

Understanding the status of small carnivores is crucial given our increasing knowledge of the important roles they play in ecosystem structure and function. As secondary consumers, small carnivores can influence ecosystem structure through top-down effects on herbivorous mammals, which in turn can affect primary producers (Roemer et al., 2009). For example, in boreal grassland and tundra ecosystems, the exclusion of small mustelids led to higher vole (Arvicolinae) densities and plant damage (Norrdahl et al., 2002; Hambäck et al., 2004). Small carnivores can also influence ecosystem structure and function through other processes, such as long-distance seed dispersal (Jordano et al., 2007) and the alteration of nitrogen and phosphorus levels in soils, which cause subsequent changes in plant assemblages and biomass (Croll et al., 2005; Maron et al., 2006; Gharajehdaghipour et al., 2016). Further, when traditional large apex predators are lost in ecosystems, persisting small carnivores can become apex and exert strong top-down pressure on large herbivores (Kilgo et al., 2012).

Small carnivores also provide numerous ecosystem services that benefit human society. In Europe, golden jackals are estimated to annually remove >13,000 tons of domestic animal waste through scavenging and >158 million crop-depredating rodents (Ćirović et al., 2016). In addition to these services, the reduction of rodent populations by small carnivores may also reduce the risk of Lyme disease (Levi et al., 2012) and rabies (Braczkowski et al., 2018) in humans. Lastly, native carnivores can help control the invasion of non-native prey species to the benefit of native prey species. In Great Britain, the pine marten (*Martes martes*) suppresses invasive gray squirrels (*Sciurus carolinensis*), which creates a refugium for native red squirrels (*S. vulgaris*) to recover (Twining et al., 2021). Thus, pine martens aid in conserving a native species and controlling an invasive one, reducing the need for expensive and logistically intensive human intervention.

Due to the clear importance of small carnivores in ecosystems, a better understanding of the extent and context of how small carnivores are responding to global change is necessary. We investigated the status and population trends of both large and small carnivores to evaluate the extent to which the two groups differ globally. We also reviewed the threats to threatened small carnivores and suggest a path forward to advance both our understanding and their conservation.

2. Methods

We utilized data from the IUCN Red List of Threatened Species (global assessment data and range data; IUCN (2020)), where we restricted our search to Taxonomy: Order/Carnivora. We then excluded species classified as extinct, and marine mammals within the families Phocidae, Otariidae, and Odobenidae. This yielded a total of 256 terrestrial and semi-terrestrial Carnivorans. We excluded pinnipeds based on our taxonomic selection criteria because they are highly adapted to life at sea, but retained the sea otter because of its taxonomic link to other semi-terrestrial otters (Estes and Bodkin, 2002). In a review of the life-history traits of 121 terrestrial and semi-terrestrial species from twelve carnivore families, Wallach et al. (2015) suggest that an apex carnivore is one that is able to self-regulate its population density, and found that an average mass of 13–16 kg marked the threshold between extrinsically-regulated and self-regulated carnivores. This weight criterion is similar to the threshold identified in previous global reviews that differentiated large from small carnivores for subsequent analysis (Prugh et al., 2009; Ritchie and Johnson, 2009; Ripple et al., 2014; Prugh and Sivy, 2020). Accordingly, we assigned an adult weight to each species using the dataset PanTHERIA (Jones et al., 2009) and defined a large carnivore as one weighing >16 kg and a small carnivore as one <16 kg. This resulted in 27 large and 229 small carnivores (Supplementary Table S1).

We first calculated the proportion of large and small carnivores that fell within each IUCN Red List status (Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT], Least Concern [LC], or Data Deficient [DD]) and population trend (Decreasing, Stable, Increasing, or Unknown) category. We then conducted two-proportions z-tests with the R function *prop.test* (R Core Team, 2020) to evaluate differences between the groups. We also extracted the year of the first IUCN assessment for each species and the total number of assessments conducted since then. For the total number received we excluded assessments that state a species is DD (or following older terminology of Indeterminate [I] or Insufficiently known [K]) under the assumption that if a species was assessed as DD, it had not been sufficiently assessed to be comparable to others. As these data were not normally distributed, we conducted an unpaired two-samples Wilcoxon test with the R function *wilcox.test* to investigate potential differences.

To focus our review of threats to large and small carnivores, we categorized species as either threatened or non-threatened. The 'threatened' group comprised species classified by the IUCN as CR, EN, or VU. The 'non-threatened' group comprised species classified by the IUCN as NT, LC, or DD. We chose to include the six DD species in the non-threatened category as two were predicted to be non-threatened (Bland et al., 2015), and one was previously classified as non-threatened by the IUCN. Further, once classified, most DD species tend to be non-threatened (Butchart and Bird, 2010; Bland et al., 2015). We then examined the specific threat types affecting threatened species by sub-setting the IUCN assessment data per threat. We also mapped the species ranges by threat to explore the spatial extent and any potential regional clustering. We acknowledge that IUCN species range maps can be inaccurate, but we use them for a broad scale inference of regional clustering across the globe. We created all figures using R version 4.0.1 and packages *ggplot2* (Wickham, 2016) for figures and *letsR* (Vilela and Villalobos, 2015) for range maps.

3. Results

We found no significant difference between the proportion of large and small carnivores listed as CR (0.04, 0.01, $\chi_1 = 0.02$ $p = 0.90$), EN (0.15, 0.09, $\chi_1 = 0.46$ $p = 0.50$), NT (0.22, 0.12, $\chi_1 = 2.46$ $p = 0.12$), or DD (0.00, 0.03, $\chi_1 = 0.03$ $p = 0.86$; Fig. 1). However, there were significantly more VU large (0.37, 0.13, $\chi_1 = 8.76$ $p < 0.01$) and significantly more LC small carnivores (0.22, 0.64, $\chi_1 = 15.99$ $p < 0.01$). There were 3, 20, and 30 small carnivores listed as CR, EN, and VU, respectively, whereas for large carnivores, there were 1, 4, and 10, respectively.

Both large and small carnivores showed similar population trends, with most populations Decreasing (Fig. 1). There was no significant difference between the proportion of Decreasing (0.70, 0.50, $\chi_1 = 3.32$ $p = 0.07$), Stable (0.15, 0.27, $\chi_1 = 0.22$ $p = 0.64$), Increasing (0.07, 0.03, $\chi_1 = 1.31$ $p = 0.25$), or Unknown (0.07, 0.20, $\chi_1 = 1.67$ $p = 0.20$) population trends between large and small carnivores, respectively.

The median (plus interquartile range [IQR]) year of the first IUCN Red List assessment for large carnivores was 1986 (IQR 1982–1996), ten years earlier than 1996 (IQR 1990–1996) for small carnivores. Further, since the date of their first assessment, large carnivores have received significantly more assessments ($W = 4543.50$, $p < 0.01$) with a median of 0.18 (0.16–0.24) assessments per year compared to small carnivores' 0.13 (0.13–0.17).

The threats listed by the IUCN for threatened large and small carnivores overlapped considerably (Fig. 3), where biological resource use and agriculture were the leading threats for both groups. Although

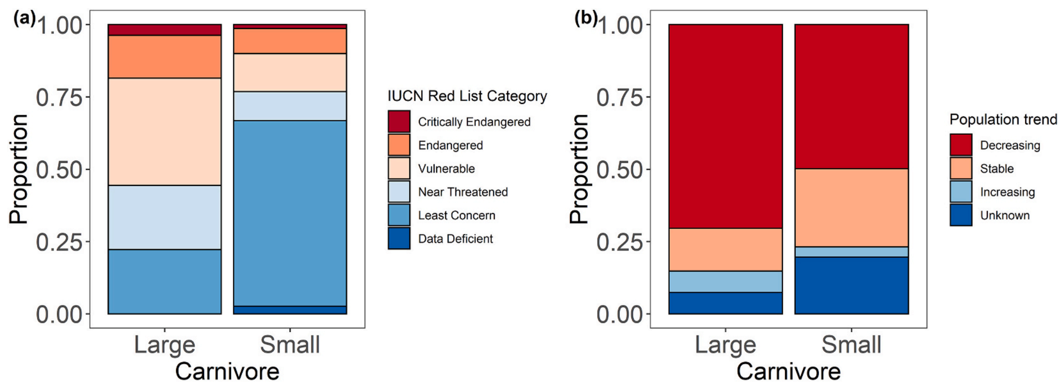

Fig. 1. The proportion of large (>16 kg; n = 27) and small (<16 kg; n = 229) carnivores categorized by (a) the IUCN Red List status and (b) the population trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Southeast Asia, sub-Saharan Africa, and Madagascar have similar levels of high species richness, Southeast Asia held a disproportionately high richness of threatened small carnivores (Fig. 2).

4. Review of major threat categories for small carnivores

Below, we review the threats that affected ≥20% of threatened small carnivores (Fig. 3). Given the overlap in their effects, we collapsed 'agriculture & aquaculture', 'residential & commercial development', 'natural systems modification', and 'transportation and service corridors' to the collective 'land use change', and 'energy production & mining' and 'pollution' to the collective 'energy production'.

4.1. Biological resource use

Biological resource use was the leading threat, affecting almost all threatened small carnivores (96%; Table 1; Fig. 3; Supplementary Table S2). For carnivores, this category mainly refers to overhunting and poaching, but the motivations for such activities differ regionally. The highest richness of species affected by biological resource use was in Southeast Asia, coinciding with the highest richness of threatened small carnivores and small carnivores overall (Fig. 2; Fig. S3a). Southeast Asia has already been identified as a priority region for species conservation (Duckworth et al., 2012; Willcox, 2020), where the main threat is hunting for illegal wildlife trade. The demand for wild meat as a luxury consumptive item has driven indiscriminate snaring, cited as the leading cause of many carnivore species declines in Southeast Asia (Willcox et al., 2014; Gray et al., 2018). Other sources of demand in Southeast Asia come from a desire to own exotic pets and for body parts to be used in traditional medicine (Sodhi et al., 2004; Nijman, 2010; Siriwat and Nijman, 2018). Importantly, population declines in the traditionally targeted, larger carnivores are likely to cause an increase in demand for other, smaller carnivores in the future (Willcox, 2020).

Although not the only wealthy region contributing to demand (e.g.

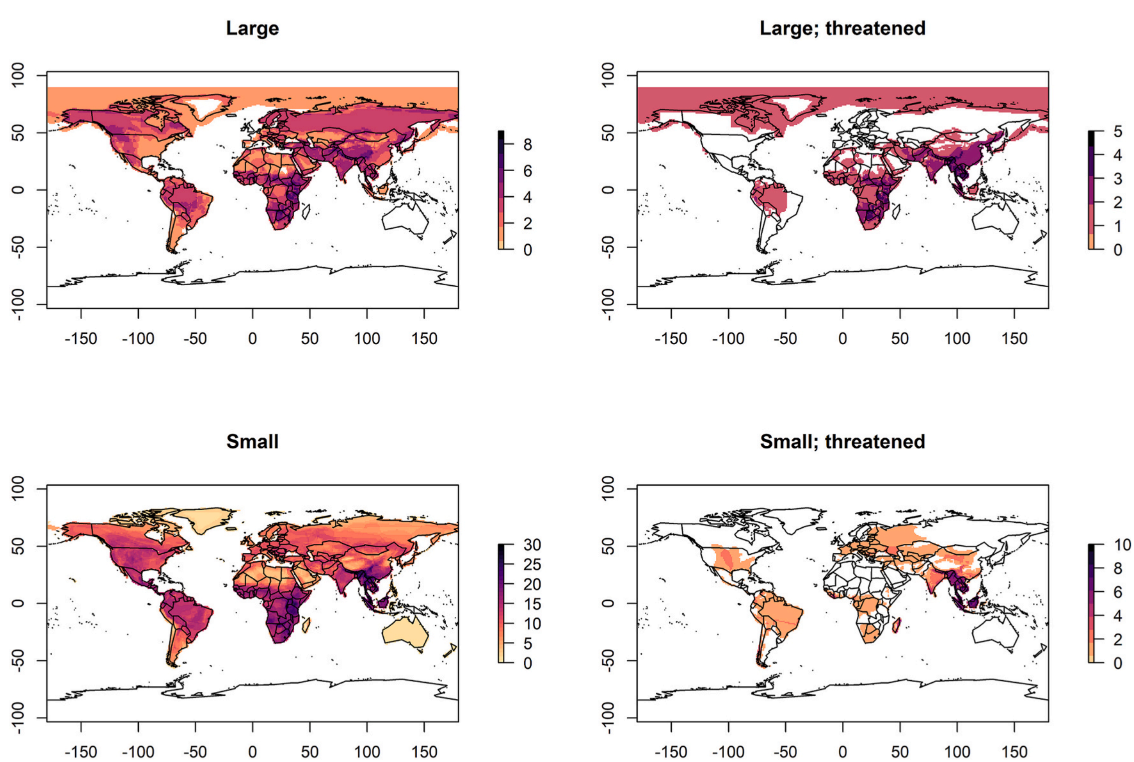

Fig. 2. Species richness of all large (>16 kg; $n = 27$) and small (<16 kg; $n = 229$) carnivores and threatened (those categorized by the IUCN Red List as CR, EN, VU) large (n = 15) and small (n = 53) carnivores. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

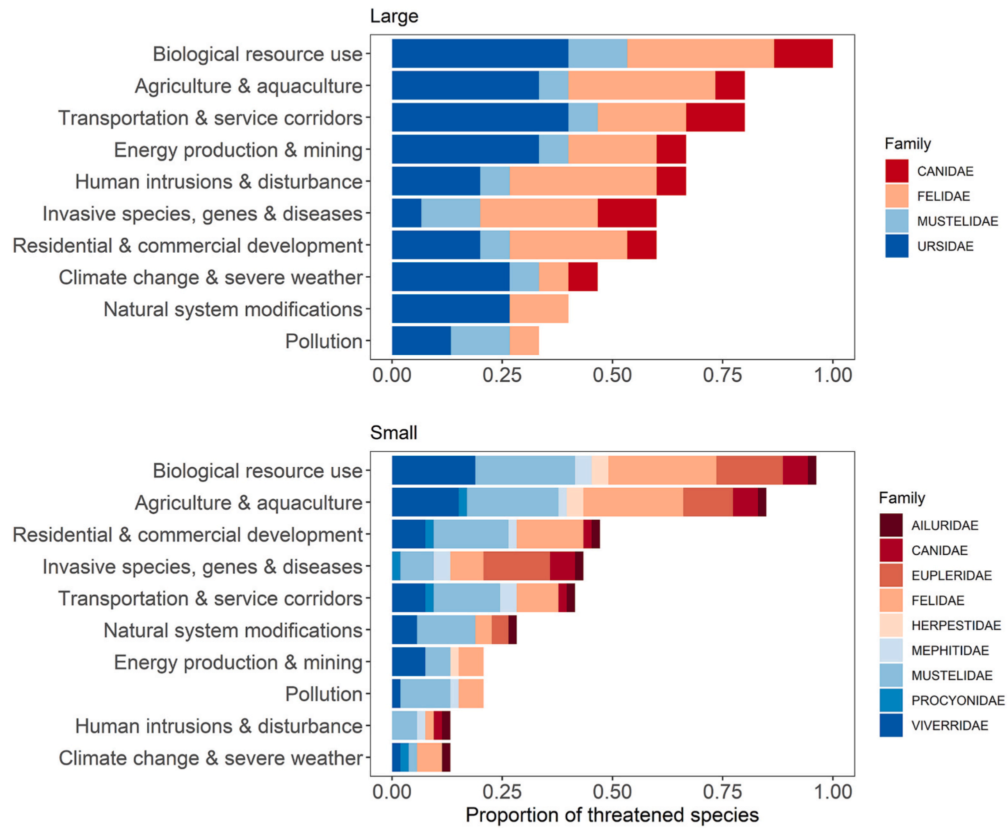

Fig. 3. The ranked threats affecting large (>16 kg; $n = 15$) and small (<16 kg; $n = 53$) threatened carnivores (those categorized by the IUCN Red List as CR, EN, VU) by family. We only display threats affecting >5% of species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

North America and Europe (Duffy, 2016; Wyatt et al., 2018)), Southeast and East Asia hold two global centers of demand (Vietnam and China) that are fueling illegal sourcing and trafficking of wildlife from across Asia. However, parts of Asia are also increasingly sourcing and trafficking wildlife in source countries from other parts of the world experiencing high levels of corruption. Demand from overseas puts pressure on countries (e.g. the Democratic Republic of the Congo) where resources are limited to combat such illegal activities (Mukwazvure and Magadza, 2014; Ripple et al., 2016). Further, these countries have their own, different motivations for hunting, which are partly caused by increasing human populations that encroach on critical habitats and result in the increased use of wildlife for subsistence (Doughty et al., 2015; Duffy et al., 2016; Knapp et al., 2017). A lack of economic opportunity within local communities can also exacerbate illegal harvest of small carnivores (Challender and MacMillan, 2014).

Of the nine families containing threatened small carnivores, Felidae made up the largest proportion of those threatened by biological resource use. Felidae is larger than most families (30 spp.) and all 13 threatened species are affected by biological resource use as they are especially vulnerable to overhunting and poaching for sale in the illegal wildlife trade. This may be a function of increased trophy hunting or commodity trade of felid pelts and other body parts (Palazy et al., 2011; Nijman et al., 2019b). A significant emerging threat is also the growing exotic pet trade, and digital platforms in particular are leading to a rapidly growing and easily accessible illegal exotic pet trade online (Siriwat and Nijman, 2018; Siriwat et al., 2019). Although this trade affects numerous small carnivores (Siriwat et al., 2019), it is particularly active for otters (Lutrinae) in Southeast Asia (Gomez and Bouhuys, 2018; Siriwat and Nijman, 2018).

4.2. *Land use change*

Land use change (a combination of the IUCN threat categories agriculture & aquaculture, residential & commercial development, transportation & service corridors, and natural system modification; Table 1; Supplementary Table S2) affected 91% of threatened small carnivores. Land use change as a result of agriculture was listed as the greatest threat, affecting 85% of threatened small carnivore species (Table 1; Supplementary Table S2). This is mostly driven by the creation of large-scale agricultural plantations and conversion to industrial agriculture. In particular, growth of the palm oil industry is predicted to expand in Southeast Asia, Africa, and South America (Fitzherbert et al., 2008), overlapping with areas containing the greatest richness of threatened small carnivores (as well as small carnivores overall; Fig. 2; Fig. S3b). The status of Eupleridae species are of particular concern in this regard as they are threatened by deforestation and are endemic to Madagascar. Deforestation and habitat conversion to create residential and commercial development occurs worldwide as a result of increasing human populations (Seto et al., 2011). While some small carnivore species are able to adapt to areas of human development (Bateman and Fleming, 2012), land conversion to residential and commercial development was listed as a threat to 47% of threatened small carnivore species (Table 1; Supplementary Table S2). Transport and service corridors impacted 42% of threatened terrestrial small carnivores (Table 1; Supplementary Table S2), while the less understood threat of natural systems modification affected 28% (Table 1; Supplementary Table S2). The impact of natural systems modifications, such as the increased severity and frequency of fires (Kinnaird and O'Brien, 1998; Thapa et al., 2018), requires further research.

Collectively, human-induced land use changes can be problematic for threatened small carnivores in several different ways. First, land use

Table 1
Threat categories and sub-categories as defined by the IUCN with the number of threatened (CR, EN, VU; n = 53 species) small carnivores affected. For a breakdown by family see Supplementary Table S2.

IUCN Red List Threat	Number of threatened small carnivores affected
Biological resource use	**51 (96%)**
Hunting & trapping terrestrial animals (intentional & unintentional)	48 (91%)
Gathering terrestrial plants (intentional & unintentional)	8 (15%)
Logging & wood harvesting (intentional & unintentional)	34 (64%)
Fishing & harvesting aquatic resources (intentional & unintentional)	8 (15%)
Agriculture & aquaculture	**45 (85%)**
Annual & perennial non-timber crops	40 (76%)
Wood & pulp plantations	24 (45%)
Livestock farming & ranching	21 (40%)
Marine & freshwater aquaculture	8 (15%)
Transportation & service corridors	**22 (42%)**
Roads & railroads	22 (42%)
Utility & service lines	1 (2%)
Shipping lanes	1 (2%)
Residential & commercial development	**25 (47%)**
Housing & urban areas	23 (43%)
Commercial & industrial areas	10 (19%)
Tourism & recreation areas	7 (13%)
Invasive and other problematic species, genes & diseases	**23 (43%)**
Invasive non-native/alien species/diseases	19 (36%)
Problematic native species/diseases	7 (13%)
Introduced genetic material	1 (2%)
Problematic species/diseases of unknown origin	1 (2%)
Viral/prion-induced diseases	7 (13%)
Diseases of unknown cause	0
Natural system modifications	**15 (28%)**
Fire & fire suppression	7 (13%)
Dams & water management/use	9 (17%)
Other ecosystem modifications	4 (8%)
Energy production & mining	**11 (21%)**
Oil & gas drilling	2 (4%)
Mining & quarrying	8 (15%)
Renewable energy	4 (8%)
Pollution	**11 (21%)**
Domestic & urban waste water	8 (15%)
Industrial & military effluents	9 (17%)
Agricultural & forestry effluents	9 (17%)
Garbage & solid waste	5 (9%)
Air-borne pollutants	0
Excess energy	2 (4%)
Human intrusions & disturbance	**7 (13%)**
Recreational activities	4 (8%)
War, civil unrest & military exercises	3 (6%)
Work & other activities	2 (4%)
Climate change & severe weather	**7 (13%)**
Habitat shifting & alteration	5 (9%)
Droughts	1 (2%)
Temperature extremes	0
Storms & flooding	1 (2%)
Other impacts	1 (2%)
Geological events	**1 (2%)**
Earthquakes/tsunamis	1 (2%)
Avalanches/landslides	1 (2%)
Other	**0**

change can cause habitat fragmentation and degradation, which in turn reduces connectivity and gene flow and can lead to isolated populations (Riley et al., 2006; Crooks et al., 2011; Gerber et al., 2012; Poessel et al., 2014). Further, fragmentation causes edge effects and degrades habitat beyond the boundary of the transformed land (Laurance et al., 2007). Second, land use change can reduce the availability of areas suitable for species' needs, such as cover for hunting or denning (Cantú-Salazar et al., 2009; Gálvez et al., 2013). Third, changes in land types can reduce prey species' populations, which in turn can negatively affect carnivores that rely on those prey species (Wolf and Ripple, 2016). Finally, conversion to human land uses can increase human-carnivore conflict (Treves and Karanth, 2003; Carvalho et al., 2018; Planillo et al., 2018). Roads have proliferated worldwide due to urban development (Aljoufie et al., 2013) and resource extraction such as logging (Wilkie et al., 2000), palm oil (Fitzherbert et al., 2008), and petroleum (Jones et al., 2015). As expansion of human activities into carnivore habitat continues, road development will increase, with 3.0–4.7 million km of roads predicted to be added to existing road networks by the year 2050 (Meijer et al., 2018). Moreover, roads increase access for hunting and poaching of carnivores and their prey (Wilkie et al., 2000; Espinosa et al., 2018; Duporge et al., 2020). This is of particular concern in countries that are small carnivore species-rich and also developing, where there is a greater risk of illegal hunting and trade (Clements et al. (2014); Fig. S3c).

4.3. Invasive species and diseases

Invasive species and diseases were listed as a threat to 43% of threatened small carnivores (Table 1; Supplementary Table S2). Invasive species have been, and are predicted to increasingly be, introduced accidentally or intentionally by humans into many ecosystems globally (Kolar and Lodge (2001); Fig. S3e). In particular, the close relationship between humans and some invasive carnivore species (such as domestic cats [*Felis catus*] and dogs [*Canis lupus familiaris*]) means that increasing human encroachment upon natural areas is likely to further negatively impact threatened small carnivores in the future (Home et al., 2018). Invasive species can negatively affect threatened small carnivores in several ways. Aided by a lack of natural predators in the ecosystems in which they are introduced, invasive species may place pressure on threatened small carnivore populations through direct competition for resources (Bonesi and Palazon, 2007; Vanak et al., 2014; Farris et al., 2017a; Farris et al., 2017b) or predation (Ritchie et al., 2014; Farris et al., 2017a). Invasive species can affect the natural behaviors or activity patterns of native small carnivores (Farris et al., 2015) and, in some cases, may also hybridize with closely related native species, potentially leading to loss of genetic variability or introgression of non-native genes into threatened small carnivore populations (Kelly et al., 1999). For example, Ethiopian wolves (*Canis simensis*) in the Bale Highlands have been documented hybridizing with domestic dogs, which threatens the genetic integrity of this endangered canid that persists in several small, isolated subpopulations (Gottelli et al., 1994; Marino and Sillero-Zubiri, 2011).

Invasive species can also introduce novel pathogens into the environment (Beltrán-Beck et al., 2012) or act as reservoirs or intermediate hosts for pathogens (Sepúlveda et al., 2014; Sutor et al., 2014) that impact small carnivores. Outbreaks of rabies, canine distemper, and other infectious diseases can lead to dramatic decreases in abundance and even regional extirpation of some threatened small carnivore populations (Thorne and Williams, 1988; López et al., 2009). In particular, rabies and canine distemper viruses are widely recognized as important threats to carnivore populations worldwide (Deem et al., 2000; Woodroffe et al., 2004) and, in some cases, epizootics of these viruses in wildlife have been found to be mediated by non-native species (Alexander and Appel, 1994; Holmala and Kauhala, 2006).

4.4. Energy production

Energy production (a combination of the IUCN threat categories energy production & mining and pollution; Table 1; Supplementary Table S2) collectively threatened 38% of small carnivores (Table 1; Supplementary Table S2). Fossil fuel exploration, and associated road development and activity, can negatively impact terrestrial wildlife by further contributing to habitat fragmentation (Sawyer et al., 2017), multi-source pollution (Monson et al., 2000), and increased human exploitation (Espinosa et al., 2018). This threat is of particular concern given fossil fuel exploration and extraction are expected to increase in the next 15 years in many species-rich areas, such as Asia-Pacific (Harfoot et al. (2018); Fig. 2; Fig. S3f). Mining can negatively impact threatened small carnivores, particularly those dependent on aquatic habitats, due to habitat destruction, sedimentation of rivers, and multi-source pollution. For example, gold mining operations frequently use mercury to recover trace amounts of gold, and unrecovered mercury accumulates in the environment (Laperche et al., 2014; Mason et al., 2019). Evidence of mercury biomagnification in aquatic food chains makes this form of chemical mining particularly detrimental to small carnivores such as North American river otters (*Lontra canadensis*) (Crowley et al., 2018). Altered flooding patterns and fragmenting of rivers as a result of hydroelectric dam construction are particularly widespread in South America and Asia (Zarfl et al., 2015), where changing river dynamics can threaten semi-aquatic carnivores (i.e. otters [Lutrinae]) because of habitat destruction and fragmentation and changes in prey availability (Santos et al., 2008).

5. Addressing knowledge gaps

The difficulties of collecting data on species with small populations and those that are Data Deficient can outweigh the incentives for studying them (Bischof et al., 2014). Smaller carnivores in particular can pose additional research challenges, such as cryptic coloration, difficulty in identifying species, and elusive behavior. Scientific journal requirements and reviewers sympathetic to small sample sizes could increase research output (dos Santos et al., 2020; Williams et al., 2020), but viable options exist for increasing knowledge of threatened species while still acquiring publishable results. Although animal captures typically provide more information on individuals, non-invasive methods are increasingly being used to monitor and study small carnivores globally (Thompson, 2013). While traditional non-invasive sampling methods (e.g. track transects and plates, scat counts and analyses, and hair snares) are still useful in some situations (but still difficult in the tropics), over the past two decades acoustic monitoring (Hansen et al., 2015) and wildlife camera traps in particular have greatly advanced our ability to gain information on carnivore distributions (Marinho et al., 2018; Watts et al., 2019), populations (Rich et al., 2019; Chatterjee et al., 2020), and behaviors (Agha et al., 2017; Windell et al., 2019). Although large, charismatic carnivores receive the most funding (Mammola et al., 2020), camera trap surveys that are designed to monitor other species (particularly those designed to monitor large predators) also capture images of small carnivores (Scotson et al., 2017; Chatterjee et al., 2020), highlighting the need for researchers to catalogue, process, validate, and use photo-encounters of non-target species. Such data can provide further insights on carnivore intraguild interactions (Mills et al., 2019; Monterroso et al., 2020) and effects on trophic structure (Suraci et al., 2016; Jiménez et al., 2019). Camera data also align well with citizen science platforms and can be easily shared to gain inference on rare or cryptic species while fostering collaboration (Swanson et al., 2015; Ahumada et al., 2019).

We also encourage researchers to design studies focused on assessing the responses of small carnivores to their key threats and how management interventions could mitigate impacts. Land use change, and associated increases in biological resource use and transportation corridor development (several of the most frequently listed threats to small carnivores in our review), are expected to continue under sustained human population growth (Powers and Jetz, 2019). Fortunately, satellite imagery (such as those available via Google Earth Engine (Gorelick et al., 2017)) and other long-term remote sensing data, when linked with on-the-ground assessments of carnivore distribution, movement, and resource use, can provide important insight into species responses to land use change at fine and coarse spatial scales (Bischof et al., 2014; Gastón et al., 2016). Importantly, some small carnivores can still persist in modified landscapes. For example, Bahaa-el-din et al. (2016) found high densities of African golden cats (*Caracal aurata*) in timber stands, and Loock et al. (2018) found a high density of servals (*Leptailurus serval*) in the area surrounding an industrialized site. Thus, there is a need to conduct species-, site-, and condition-specific investigations into the complex suite of factors that can influence the ecology of small carnivores in a changing environment (Roemer et al., 2009; Jachowski et al., 2020). Ultimately, without robust scientific information on species-level threats and their subsequent effects, it is difficult to implement meaningful conservation actions targeted at small carnivores.

Biological resource use is the leading (or at least most prominently listed) threat to small carnivores, mainly as a result of hunting occurring at an unsustainable rate. As such, evaluating the social drivers (e.g. attitudes and tolerance) behind these behaviors is critical to future global conservation (St John et al., 2011; St John et al., 2012; Treves and Bruskotter, 2014). For example, to prioritize conservation actions for carnivores in human-dominated landscapes, Gálvez et al. (2018) recently proposed a modeling framework that integrates social and ecological data collected at the same spatial scale to assess how human-predator relations may interact in space and time. Going forward, we believe such interdisciplinary approaches that integrate animal ecology and behavior with social, political, and economic sciences are, in most circumstances, essential to inform effective conservation initiatives.

6. Next steps for advancing global small carnivore conservation

We believe there are five key steps to advancing small carnivore conservation in the face of rapid global change. First, given IUCN Red List assessments are a primary driver of global increases in scientific knowledge, public awareness, funding and resources, and targeted action towards the conservation of listed species (Betts et al., 2020), we suggest more frequent IUCN Red List assessments of small carnivores are needed. While particular attention should be given to those species deemed DD ($n = 6$) and CR ($n = 3$), all threatened small carnivores ($n = 53$) would benefit from more frequent assessments that are at least on par with large carnivores. The amount of conservation research on terrestrial mammals is best explained by the scientific capacity of countries in which species occur (dos Santos et al., 2020). Therefore, to better inform these more frequent assessments, there is a need to increase the research capacity of biodiverse countries through monetary and resource investments to help combat the taxonomic bias we report in carnivore conservation.

Second, our findings suggest Southeast Asia is a particularly important region to focus conservation efforts based on threatened status and population trends (Duckworth et al., 2012; Willcox, 2020). In addition, our findings support previous calls for conservation attention to be placed on decreasing population trends in small carnivores within northern South America (Schipper et al., 2009), as well as addressing unknown population trends of small carnivores in sub-Saharan Africa (Do Linh San and Somers, 2013). In particular, native carnivores on Madagascar are endemic and recent evidence suggests carnivores here are in particular conservation need (Farris et al., 2017a; Farris et al., 2017b). In addition, it has been suggested that there are regional trends in the willingness of IUCN assessors to assign “Unknown” as opposed to a specific population trend status, which should be considered when trying to compare trends among regions (W. Duckworth, IUCN SSC Red List Authority Coordinator for small carnivores, pers. comm.). Moreover, IUCN assessors can list either all known threats and their corresponding severity, or only major threats with no corresponding severity. Thus, interpreting and comparing threats across species and regions can be difficult as the exact methodology for each is unknown. We suggest that IUCN assessment reports become more structured moving forward to assist in repeatability and subsequent comparisons. Regardless, our findings suggest areas of high small carnivore species richness in tropical latitudes (i.e. Southeast Asia, South America, sub-Saharan Africa, and Madagascar) are in greatest need of both investigations into population ecology and conservation attention.

Third, it is evident that, given the near-global distribution of threatened small carnivores, there is a need to directly investigate ways to mitigate the main local threats to these species in most ecosystems globally. While continued infrastructure development in the Anthropocene is inevitable, there are strategies that can be employed to lessen the impacts of biological resource use and land use change. Transformed regions, such as those cleared for agriculture, can still be valuable areas for small carnivores, even species conventionally considered poor adapters to anthropogenic change (Bahaa-el-din et al., 2016; Loock et al., 2018), which can provide ecosystem services such as pest control in return (Ćirović et al., 2016). Thus, research is needed on how sustainable development practices can promote conservation of small carnivores. For example, conserving water bodies, ensuring connectivity between patches, and manual harvesting of crops during non-crepuscular hours could all promote conservation and coexistence of carnivores in palm oil landscapes (Payán and Boron, 2019). In regard to road networks, with knowledge on animal movement patterns, measures can be identified to minimize the density of roads (Rhodes et al., 2014) but, most importantly, attention should be placed on preventing the use of roads for illegal offtake.

Fourth, the exploitation of small carnivores is likely one of the most difficult threats to address as it has several contributing factors, such as human consumption, commodity trade, and persecution, which incorporate social, economic, and ethical issues. Although 49% of small carnivores are protected by CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), international regulations alone have not halted this pressing threat to small carnivores (Trouwborst, 2015; Siriwat et al., 2019). Given the number of actors, reducing illegal wildlife trade requires a combination of decreasing demand as well as increased regulation, enforcement, and community engagement (Phelps et al., 2016). Regulatory policy exists for carnivores in many regions of the world, yet enforcement is often lacking (Yi-Ming et al., 2000; Nijman et al., 2019a) and recent efforts have highlighted the benefit of incentivizing enforcement at the local community level (Cooney et al., 2017). Many carnivore uses are also tied to cultural and/or religious practices (Alves et al., 2010; Alves and Alves, 2011), so enforcement must be both realistic and considerate of cultural and religious beliefs. By contrast, where wildlife are taken for consumption, poverty alleviation and increased food security rather than increased regulation could be more effective (Challender and MacMillan, 2014). Although not universal, promoting food security in some countries may help reduce overhunting, by-catch from snares, and consumption (Lindsey et al., 2013). Collectively, to sustainably reduce biological resource use, it is evident that complex and often site- or region-specific socio-cultural factors need to considered when drafting and implementing legal protection (Cawthorn and Hoffman, 2015).

Fifth, conservationists should work to increase the greater public understanding and appreciation of the ecological roles and services provided by small carnivores in order to encourage their conservation. This can be justified not only in the intrinsic ethical (and often legally mandated) right for any threatened small carnivore species to receive conservation attention akin to large carnivores of comparable threat level, but because they are likely to become increasingly important in ecosystem structure and function in the future if large species are locally or regionally extirpated. After several decades of global trophic downgrading (Estes et al., 2011), large carnivores are recovering and stable in some areas, but that does not mean they exert the same strength of top-down effects they did previously (Kuijper et al., 2016). In some areas, large carnivore recovery is unlikely to occur (Cardillo et al., 2004; Wolf and Ripple, 2017), allowing small, formerly non-apex, carnivores to ascend to the status of apex carnivores in some ecosystems, such as coyotes (*Canis latrans*) in North America (Gehrt et al., 2013; Cherry et al., 2016). This shifting in both assembly and trophic baselines of carnivore communities is not new; what we consider an apex carnivore today happened relatively recently (Pardi and Smith, 2016; Smith et al., 2016). However, we should expect future shifts to happen more quickly under the current rapid rate of global change (Berger et al., 2020).

7. Conclusions

Our results show that small carnivores are similarly endangered with extinction globally as are large carnivores, despite differences in attention. More small carnivore species were threatened (i.e. CR, EN, VU; 53/229) than large carnivores (15/27), and nearly five times as many small carnivores are endangered with extinction (i.e. CR, EN; 23/27), compared to large (5/27) carnivores. Proportionally, the number of threatened (i.e. CR, EN and VU) small carnivores (23%) was similar to that of all mammals (24%; Frick et al. (2019)). In addition, our findings do not provide support for mesopredator release occurring at a global scale, where we observed paralleled declining population trends between large and small carnivores. We highlight Southeast Asia as a particular conservation priority, because it holds the highest number of threatened small carnivores and also overlaps with a high number of threatened large carnivores. Even though the threats they face are similar, small carnivores have received fewer IUCN assessments than have large carnivores, highlighting a knowledge disparity within the guild and the need for more frequent assessments of small carnivores. Perhaps most concerning, the two major threats to small carnivores (biological resource use and land use change) are likely to increase globally (Bell et al., 2004; Willcox, 2020), suggesting that the number of small carnivore species listed as Vulnerable could grow rapidly due to increasing human pressure (FAO, 2010; Li et al., 2015; Willcox, 2020) and human population density (Ganivet, 2020). Ultimately, research and conservation attention are required to recover threatened small carnivore species and slow or reverse current declines before these threats become too large to mitigate.

Declaration of competing interest

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial or non-financial interest in the subject matter or materials discussed in this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109005.

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