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A global assessment of large terrestrial carnivore kill rates

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ABSTRACT

Through killing and instilling fear in their prey, large terrestrial carnivores shape the structure and function of ecosystems globally. Most large carnivore species have experienced severe range and population declines due to human activities, and many are now threatened with extinction. Consequently, the impacts of these predators on food webs have been diminished or lost completely from many ecosystems. Kill rates provide a fundamental metric for understanding large carnivore ecology and assessing and comparing predation within and across ecological communities. Our systematic review of large terrestrial mammalian carnivore kill rates reveals significant positive geographic (North America, Europe, and Africa) and taxonomic (grey wolf *Canis lupus*, puma *Puma concolor*, lion *Panthera leo*, and Eurasian lynx *Lynx lynx*) bias, with most studies apparently motivated by human–carnivore conflict over access to ungulate prey and wildlife management objectives. Our current understanding of the behaviour and functional roles of many large carnivore species and populations thus remains limited. By synthesising and comparing kill rates, we show that solitary carnivores (e.g. brown bears *Ursus arctos* and most felids) exhibit higher *per capita* kill rates than social carnivores. However, ungulate predation by bears is typically limited to predation of neonates during a short period. Lower *per capita* kill rates by social carnivores suggests group living significantly reduces energetic demands, or, alternatively, that group-living carnivores defend and consume a greater proportion of large prey carcasses, or may acquire more food through other means (e.g. scavenging, kleptoparasitism) than solitary hunters. Kill and consumption rates for Canidae – measured as kilograms of prey per kilogram of carnivore per day – are positively correlated with body mass, consistent with increasing energy costs associated with a cursorial hunting strategy. By contrast, ambush predators such as felids show an opposite trend, and thus the potential energetic advantage of an ambush hunting strategy for carnivores as body mass increases. Additionally, ungulate kill rates remain relatively constant across solitary felid body sizes, indicative of energetic constraints and optimal foraging. Kill rate estimates also reveal potential insights into trophic structuring within carnivore guilds, with subordinate carnivores often killing more than their larger counterparts, which may be indicative of having to cope with food losses to scavengers and dominant competitors. Subordinate carnivores may thus serve an important role in provisioning food to other trophic levels within their respective ecosystems. Importantly, kill rates also clarify misconceptions around the predatory behaviour of carnivores (e.g. spotted hyaenas *Crocuta crocuta* and wolverines *Gulo gulo* are often considered scavengers rather than the capable hunters that they are) and thus the potential impacts of various carnivore species on their ecological communities. Despite the importance of kill rates in understanding predator–prey interactions, their utility is not widely recognised, and insufficient research limits our ability to fully appreciate and predict the consequences of modified predation regimes, justify current management actions affecting carnivores, or inform effective conservation measures. Together with other important research on predator–prey interactions, robust kill rate studies that address the research deficiencies we highlight will provide a deeper understanding of the foraging behaviours and potential ecosystem impacts of many of the world's carnivores, thus aiding effective conservation and management actions.

Key words: kill frequency, kill interval, predation, predator–prey interactions, bioenergetics, foraging, diet, carnivore management.

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I. INTRODUCTION

Through predation and fear-induced changes to prey behaviour, large-bodied carnivores perform a pivotal role in shaping the composition of communities and ecosystem processes globally (Estes *et al.*, 2011; Ripple *et al.*, 2014; DeLong *et al.*, 2015). Large carnivores, however, are also among the most threatened taxa due to habitat modification and destruction, prey depletion, and direct persecution resulting from human–wildlife conflict (Ripple *et al.*, 2014). The historic loss, and in some regions the resurgence of large terrestrial carnivores, presents unique social, economic, political, conservation, and management challenges (Treves & Karanth, 2003; Chapron & López-Bao, 2014; Chapron *et al.*, 2014). Effectively managing and overcoming these challenges requires a comprehensive understanding of the complex web of interactions within ecological communities. Kill rates, typically measured as the number of prey killed per individual predator per unit time, provide a key metric for understanding these ecological interactions. Kill rates facilitate the study of predator–prey interactions across diverse taxonomic groups and ecosystems, and enable an understanding of the influence of other factors including human activities and disturbance on these interactions (Nilsen *et al.*, 2009; Vucetich *et al.*, 2011; Gervasi *et al.*, 2012; Wittmer, Elbroch & Marshall, 2013; Smith, Wang & Wilmers, 2015). Estimating and understanding the factors that drive variation in species' kill rates can enhance our comprehension of complex species interactions within multi-species systems (Tallian *et al.*, 2017; Prugh & Sivy, 2020; Allen, Elbroch & Wittmer, 2021), and provide valuable information to ecologists, conservation practitioners (Jethva & Jhala, 2004; Wittmer *et al.*, 2013), and game and livestock managers (Power, 2002; Mattisson, Odden & Linnell, 2014).

Given the fundamental importance of kill rates for understanding carnivore foraging and the ecological impacts of predation, here we provide the first comprehensive global systematic review and synthesis of studies that have either quantified large carnivore kill rates or reported data from which relevant kill rates could be calculated. Based on transparent criteria (Haddaway *et al.*, 2015) (see online Supporting Information, Appendix S1) we conducted literature searches for 31 species belonging to seven mammalian families: Canidae, Felidae, Ursidae, Hyaenidae, Mustelidae, Eupleridae, and Dasyuridae (Table 1). We restricted our review to large terrestrial mammalian carnivore species with a mean adult body mass of ≥15 kg (Ripple *et al.*, 2014) that kill vertebrate prey. We included three additional species with mean body masses of <15 kg because of their identified role as "apex" predators within their respective ecosystems (coyote, wolverine, fossa; see Table 1 for scientific names), and one species not belonging to the order Carnivora, the Tasmanian devil, the largest extant marsupial predator. Twenty-one species were obligate carnivores, and 10 species were omnivores (Table 1). Most species (74%, $N = 23$) are experiencing population declines, and 19 (61%) are recognised by either international or national regulatory organisations as threatened with extinction (Table 1). We excluded from our review semi-aquatic mammals such as pinnipeds or otters, as well as species such as giant pandas (*Ailuropoda melanoleuca*) that have a predominantly herbivorous diet.

Drawing on nine decades of research, our synthesis highlights insights into carnivore ecology as well as shortcomings in current knowledge, including geographic and species biases in kill rate research. We offer ecological rationales for the synthesised results and consider potential environmental and ecosystem consequences if the ecological functions of large carnivores continue to be absent or diminished. Moreover, we identify future research priorities and emphasise the important role of kill rate research in elucidating some of the ecosystem impacts of global change and addressing conservation challenges, particularly human–carnivore conflict.

Table 1. List of large terrestrial carnivore species considered for this review, with their family, mean body mass (kg), diet, status, population trend, and the number of relevant unique kill rate studies included in the review. Body masses are from Ripple *et al.* (2014), Gittleman (1985), Hunter & Barrett (2018), and Rose *et al.* (2017). Diet types are from Hunter & Barrett (2018): M = meat eater; O = omnivore. Species status and trend are from the IUCN *Red List* (IUCN, 2022) and Department of the Environment (*Canis dingo*) (The Australian Government Department of the Environment, 2023): LC = least concern; NT = near threatened; VU = vulnerable; EN = endangered; CR = critically endangered; ↓ = decreasing; ↑ = increasing; − = stable;? = unknown. Table adapted from Ripple *et al.* (2014).

Family/species	Common name	Mass (kg), diet	Status (trend)	Number of relevant unique kill rate studies
Felidae				
Panthera tigris	Tiger	161, M	EN (↓)	4
Panthera leo	Lion	156, M	VU (↓)	23
Panthera onca	Jaguar	87, M	NT (↓)	2
Acinonyx jubatus	Cheetah	59, M	VU (↓)	5
Panthera pardus	Leopard	53, M	VU (↓)	10
Puma concolor	Puma	52, M	LC (↓)	38
Panthera uncia	Snow leopard	33, M	VU (↓)	2
Neofelis nebulosa	Clouded leopard	20, M	VU (↓)	0
Neofelis diardi	Sunda clouded leopard	20, M	VU (↓)	0
Lynx lynx	Eurasian lynx	18, M	LC (–)	15
Canidae				
Canis lupus	Grey wolf	33, M	LC (–)	63
Canis rufus	Red wolf	25, M	CR (↓)	0
Chrysocyon brachyurus	Maned wolf	23, O	NT (?)	0
Lycaon pictus	African wild dog	22, M	EN (↓)	7
Cuon alpinus	Dhole	16, M	EN (↓)	1
Canis dingo	Dingo	15, M	VU (↓)	0
Canis simensis	Ethiopian wolf	15, M	EN (↓)	0
Canis latrans	Coyote	13, O	LC (↑)	7
Ursidae				
Ursus maritimus	Polar bear	365, M	VU (?)	0
Ursus arctos	Brown bear	299, O	LC (–)	8
Ursus americanus	American black bear	111, O	LC (↑)	2
Tremarctos ornatus	Andean bear	105, O	VU (↓)	0
Ursus thibetanus	Asian black bear	104, O	VU (↓)	0
Melursus ursinus	Sloth bear	102, O	VU (↓)	0
Helarctos malayanus	Sun bear	46, O	VU (↓)	0
Hyaenidae				
Crocuta crocuta	Spotted hyaena	52, M	LC (↓)	3
Hyaena brunnea	Brown hyaena	43, O	NT (–)	1
Hyaena hyaena	Striped hyaena	27, O	NT (↓)	0
Mustelidae				
Gulo gulo	Wolverine	12, M	LC (↓)	1
Eupleridae				
Cryptoprocta ferox	Fossa	7, M	VU (↓)	0
Dasyuridae				
Sarcophilus harrisii	Tasmanian devil	8, M	EN (↓)	0

II. LARGE CARNIVORE KILL RATE STUDIES

Our systematic literature search identified at least 4542 unique articles, of which 196 included kill rate data meeting our search criteria (Appendix S1; Fig. S1). These papers detailed 192 unique species-specific kill rate studies (Tables S1–S4; Data S1) for 17 (54.8%) of the 31 large carnivore species we considered (Table 1). At least one kill rate estimate was extracted or calculated from 175 studies described in 178 articles and used in the subsequent kill rate syntheses (Data S1 and S2). The oldest study that met our search criteria was conducted on pumas (also commonly known as cougars and mountain lions, but puma is the most widely used vernacular globally; Wood *et al.*, 2021) in Utah, USA, in 1949 (Connolly Jr., 1949), but it was not until the 1970s that kill rate research increased considerably (Fig. 1D).

(1) Geographic distribution of kill rate studies

Overall, kill rate studies have been conducted across 27 countries and 5 continents (Fig. 1A) with most in North America ($N = 106$, 55.2%), south-eastern Africa ($N = 46$, 24.0%),

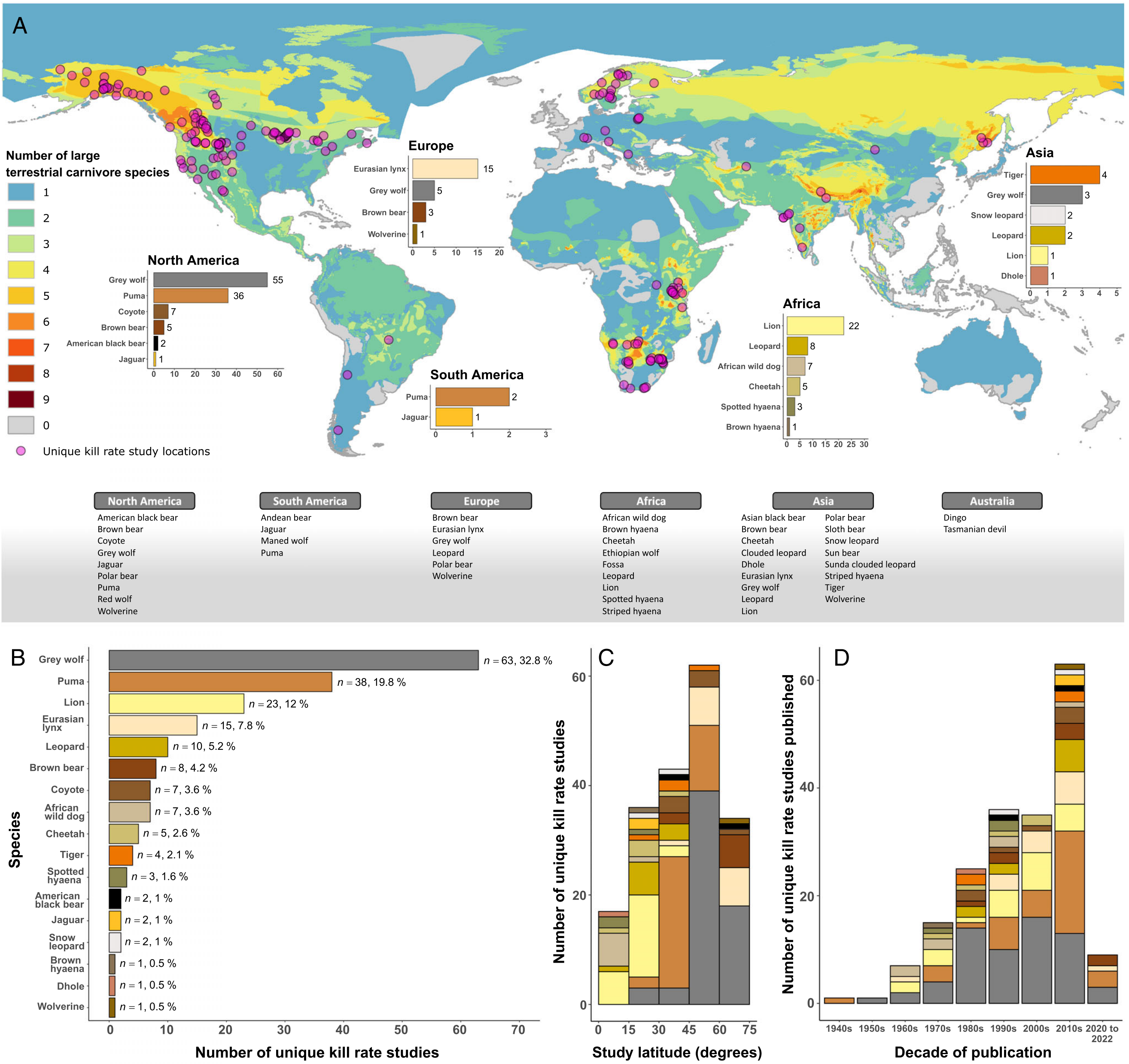


Fig. 1. Geographic distribution of large carnivore kill rate studies and research effort per species. (A) Locations of unique kill rate studies relative to current frequency distribution of large carnivore species globally (adapted from Ripple *et al.*, 2014). Number of studies per species per continent is displayed in the bar charts. Large carnivore species considered in this review are listed per continent. See Fig. S2 for individual species range maps. Species distributions are from the IUCN *Red List* (IUCN, 2022), dingo distribution adapted from (Cairns *et al.*, 2018), ESRI World Continents are from ESRI (2013). (B) Number of unique kill rate studies per species including proportion of all 192 studies. (C) Number of unique kill rate studies per species (colour coded as in B) relative to absolute latitude of study location. (D) Number of unique kill rate studies per decade of publication relative to each species (colour coded as in B). Some publications are represented more than once if they reported kill rate data for more than one species.

and Scandinavia ($N = 15$, 7.8%) (Fig. 1A; Tables S1–S4). Even after accounting for the number of large carnivore species per continent, the frequency of kill rate studies differed significantly ($p < 0.05$ using Monte Carlo chi-squared goodness-of-fit tests with simulated p-value; Appendix S1). There was an overrepresentation of studies from North America ($\chi^2 = 25.78$, $N = 23$, $p = 0.0002$; Tables S5 and S6), with the majority of North American studies undertaken in the USA (73 studies, 68.9% of North American studies; Table S2). Kill rate studies were frequently conducted in areas where active management and conservation of carnivores and ungulates occurs, or where large carnivores are considered important for tourism (e.g. South African national parks and game reserves).

Large carnivores in several regions remain understudied in terms of kill rate research. Asia represents a significant blind spot with only 13 (6.8%) kill rate studies across six species (Table S1), despite it representing the largest land mass and containing the highest number of large carnivore species of any continent included in this review ($N = 17$, 54.8%; Fig. 1A). Thirteen Asian carnivore species are known to kill, or are capable of killing, medium to large vertebrate prey (Hunter & Barrett, 2018) (Table 1). Furthermore, we only documented three (1.6%) studies in South America, despite the extensive distribution of pumas and jaguars on this continent (Fig. 1A; Table S1; see Fig. S2 for individual species range maps).

Large carnivores occur across all 14 terrestrial biomes and kill rate studies have been conducted in 12 (86%) of these, yet the geographic distribution of kill rate studies demonstrates that most research (91% of studies) has been conducted at moderate latitudes of >15 degrees (absolute latitude, i.e. north or south) (Fig. 1C) and within cold, temperate, or non-forested biomes (94% of studies) (Fig. 2A, B). After accounting for the number of large carnivore species considered in this study per biome, only the number of studies conducted in the boreal forests/taiga biome were disproportionately higher than would be expected ($\chi^2 = 32$, $N = 24$, $p = 0.0038$; Tables S7 and S8).

A higher number of kill rate studies within a biome often coincided with biomes representing a greater proportion of a large carnivore species' global distribution. However, for multiple species, certain biomes were over- or under-represented by kill rate studies relative to the proportion a biome contributed to the global distribution of a species (Fig. 2B; Tables S9–S25). In addition to management and tourism interests, research effort across study locations and biomes has likely been influenced by the high costs and practical limitations of studying large carnivores, thus restricting research and subsequent understanding of their ecological roles across parts of their geographic distribution (dos Santos *et al.*, 2020). Furthermore, the often inaccessible tropical forests near the equator, and absence of roads or suitable substrate for tracking, have probably imposed additional impediments to undertaking kill rate studies in these conditions (Cavalcanti & Gese, 2010), which may partly explain the limited kill rate research within the three tropical forests biomes (Fig. 2).

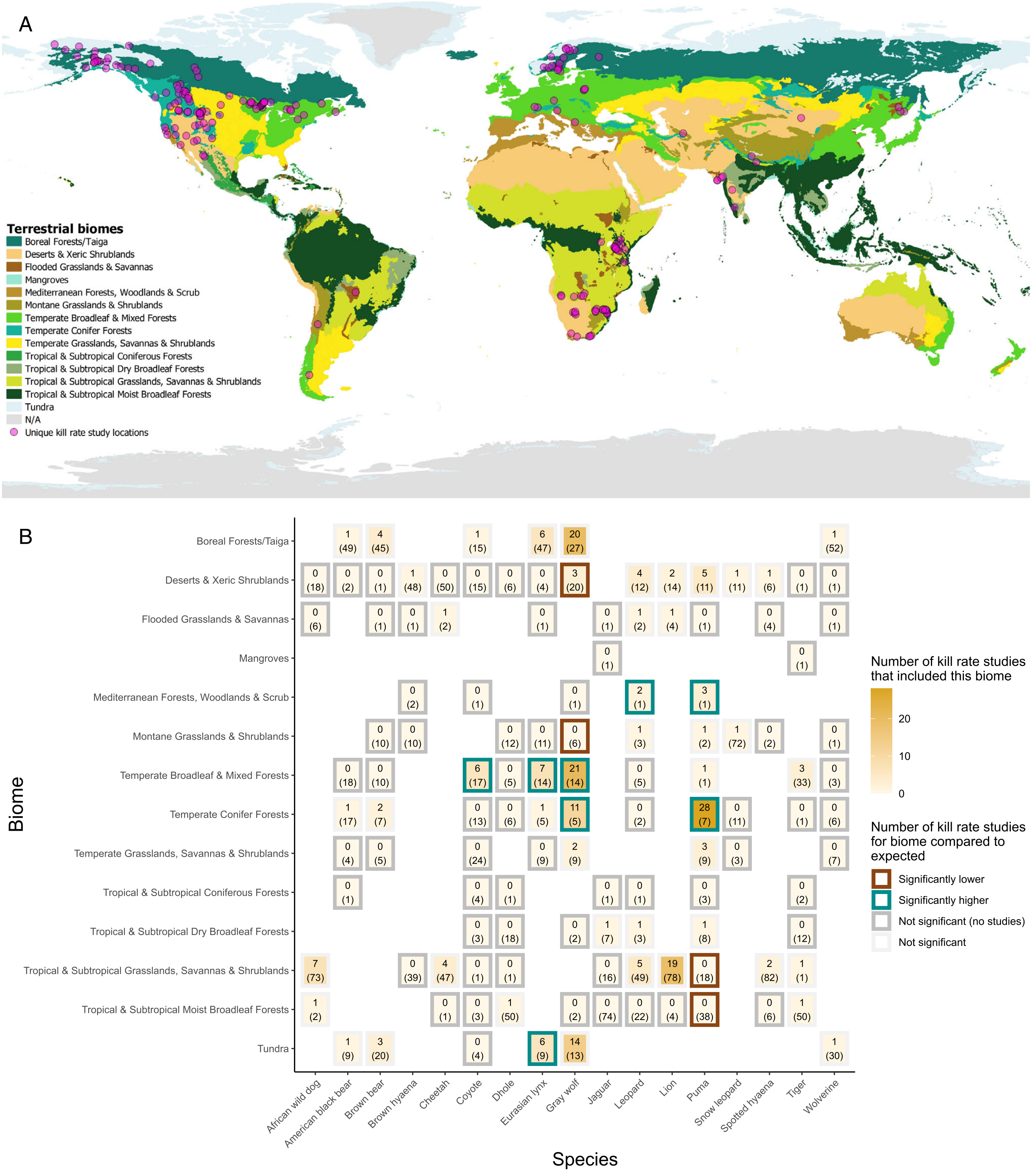
(2) Distribution of kill rate studies across species

Kill rate studies are laborious, time consuming, and costly and therefore the number of studies conducted can be considered impressive, particularly for the four best-studied large carnivore species: the grey wolf ($N = 63$, 32.8%), puma ($N = 38$, 19.8%), lion ($N = 23$, 12.0%), and Eurasian lynx ($N = 15$, 7.8%) (Table 1; Fig. 1B), which together represent 72.4% (139 of 192) of kill rate studies. However, the focus on these four species has resulted in an uneven distribution of research effort, and this pattern of certain species receiving research priority is repeated across most continents (Tables S26–S30). When considering only the large carnivore species for which kill rate studies have been undertaken, grey wolf, puma, and lion are overrepresented ($\chi^2 = 382.99$, $N = 192$, $p = 0.0001$; Table S31), while studies for Eurasian lynx are significantly greater than for other European large carnivore species ($\chi^2 = 41$, $N = 24$, $p = 0.0001$; Table S28). For some species like the grey wolf, puma, and Eurasian lynx, this discrepancy in research effort may be partly explained by the broad distribution of these species relative to other large carnivore species (Fig. S2). Although rarely indicated explicitly within articles, the uneven distribution of research effort across carnivore species also appears to have been driven by wildlife management objectives that (*i*) attempt to ensure hunting access to ungulates for humans (e.g. Ballard, Whitman & Gardner, 1987; Ballard *et al.*, 1997; McNay & Ver Hoef, 2001), (*ii*) address human–carnivore conflict over livestock (e.g. Mattisson *et al.*, 2014; Meena *et al.*, 2011), and (*iii*) address concerns regarding carnivore carrying capacity and prey stocking rates within managed game reserves (e.g. Power, 2002; Lehmann *et al.*, 2008).

By contrast, few kill rate studies have been undertaken for most other large carnivore species (Table 1; Fig. 1B) ($\chi^2 = 856.51$, $N = 192$, $p = 0.0001$; Table S32), thus restricting our understanding of their foraging ecology and limiting insights that could be gained from comparisons across species. We did not find kill rate studies for 14 of the 31 (45%) large carnivore species when conducting our review, and we documented only one to three studies for a further seven species (Table 1; Fig. 1B). The lack of kill rate studies is not surprising for omnivores such as sloth bear and sun bear (Hunter & Barrett, 2018) that rarely hunt, however, for more carnivorous species including Andean bear, Asiatic black bear, maned wolf, striped hyaena, Ethiopian wolf (Hunter & Barrett, 2018), and the Tasmanian devil (Andersen *et al.*, 2020), kill rate studies would be useful for understanding their ecological roles and determining their possible impact on wild and domestic prey. Six species that lack kill rate data are recognised as apex predators that likely have a significant impact on prey populations and their ecological communities: fossa, dingo, red wolf, clouded leopard, Sunda clouded leopard, and polar bear (Table 1). These six species are classified as "vulnerable" to extinction, and in the case of the red wolf, "critically endangered" (IUCN, 2022; The Australian Government Department of the Environment, 2023) (Table 1).

Deficiencies in kill rate research for many large carnivore species closely mirrors a lack of understanding of the impact these species can have on food webs and the functioning of ecosystems (Ripple *et al.*, 2014). Kill rate studies can provide insight into the predatory behaviours of carnivores and help clarify potential misconceptions. For example, spotted hyaenas and wolverines are often described as scavengers rather than active predators, and whilst both species are indeed facultative scavengers (Kruuk, 1972;

Mattisson *et al.*, 2016), synthesised kill rates show both species are also capable hunters, with kill rates comparable to other large carnivore species (see Section III). Even for relatively well-studied species of large carnivores, for which we may assume we have a comprehensive understanding of their ecology, multiple important knowledge gaps may still exist (LaBarge *et al.*, 2022). Hence it is important to interrogate our current level of understanding, even for



Biome	African wild dog	American black bear	Brown bear	Brown hyaena	Cheetah	Coyote	Dhole	Eurasian lynx	Gray wolf	Jaguar	Leopard	Lion	Puma	Snow leopard	Spotted hyaena	Tiger	Wolverine
Boreal Forests/Taiga		1 (49)	4 (45)			1 (15)		6 (47)	20 (27)								1 (52)
Deserts & Xeric Shrublands	0 (18)	0 (2)	0 (1)	1 (48)	0 (50)	0 (15)	0 (6)	0 (4)	3 (20)		4 (12)	2 (14)	5 (11)	1 (11)	1 (6)	0 (1)	0 (1)
Flooded Grasslands & Savannas	0 (6)		0 (1)	0 (1)	1 (2)			0 (1)		0 (1)	1 (2)	1 (4)	0 (1)		0 (4)		0 (1)
Mangroves										0 (1)						0 (1)	
Mediterranean Forests, Woodlands & Scrub				0 (2)		0 (1)			0 (1)		2 (1)		3 (1)				
Montane Grasslands & Shrublands			0 (10)	0 (10)			0 (12)	0 (11)	0 (6)		1 (3)		1 (2)	1 (72)	0 (2)		0 (1)
Temperate Broadleaf & Mixed Forests		0 (18)	0 (10)			6 (17)	0 (5)	7 (14)	21 (14)		0 (5)		1 (1)			3 (33)	0 (3)
Temperate Conifer Forests		1 (17)	2 (7)			0 (13)	0 (6)	1 (5)	11 (5)		0 (2)		28 (7)	0 (11)		0 (1)	0 (6)
Temperate Grasslands, Savannas & Shrublands		0 (4)	0 (5)			0 (24)		0 (9)	2 (9)				3 (9)	0 (3)			0 (7)
Tropical & Subtropical Coniferous Forests		0 (1)				0 (4)	0 (1)			0 (1)	0 (1)		0 (3)			0 (2)	
Tropical & Subtropical Dry Broadleaf Forests						0 (3)	0 (18)		0 (2)	1 (7)	1 (3)		1 (8)			0 (12)	
Tropical & Subtropical Grasslands, Savannas & Shrublands	7 (73)			0 (39)	4 (47)	0 (1)	0 (1)			0 (16)	5 (49)	19 (78)	0 (18)		2 (82)	1 (1)	
Tropical & Subtropical Moist Broadleaf Forests	1 (2)				0 (1)	0 (3)	1 (50)		0 (2)	0 (74)	0 (22)	0 (4)	0 (38)		0 (6)	1 (50)	
Tundra		1 (9)	3 (20)			0 (4)		6 (9)	14 (13)								1 (30)

(Figure 2 legend continues on next page.)

species and fields of research that we may consider somewhat saturated, including large carnivore foraging ecology.

III. COMPARING KILL RATES ACROSS MULTIPLE METRICS

(1) Limitations of comparing typical kill rates

Kill rates can be influenced by multiple concurrent factors such as predator age, sex or social/reproductive status (Knopff *et al.*, 2010; Mattisson *et al.*, 2011*b*; Clark *et al.*, 2014), as well as human disturbance (Smith *et al.*, 2015), competition with dominant competitors (Tallian *et al.*, 2017; Allen *et al.*, 2021), prey-to-predator ratio, predator group size (Sand *et al.*, 2012*a*), climate (Nilsen *et al.*, 2009), season, and prey size, vulnerability and availability (Sand *et al.*, 2008; Knopff *et al.*, 2010; Knamiller, 2011; Metz *et al.*, 2012). This subsequently complicates comparisons of typical kill rates (i.e. number of prey killed per predator or group of predators per unit of time) within and across species and systems. Instead, more standardised metrics such as biomass kill or consumption rates (as we provide and discuss later) provide more suitable comparisons of predator foraging requirements and behaviours. However, typical kill rates do indicate approximately how often carnivores make a kill and provide a measure of the rate at which carnivores remove individuals from prey populations, thus they are of interest to wildlife managers and ecologists. Although kill rates alone provide limited insight into predation impacts on prey populations (Vucetich *et al.*, 2011), their utility in this regard for conservation and management can be found when integrated with data on predator and prey abundance, and prey survival and reproductive rates (e.g. Jonzen *et al.*, 2013; Støen *et al.*, 2022). Moreover, examining the relationship between *per capita* kill rates across a gradient of prey density (i.e. functional response; Holling, 1959), whilst accounting for various factors of influence, is fundamental to understanding the importance of predation to predator–prey population dynamics and stability (Sinclair, 2003; Nilsen *et al.*, 2009; Dunn & Hovel, 2020), and predicting the impacts of a warming climate on these dynamics (Rall *et al.*, 2012).

Although multiple factors are capable of impacting carnivore foraging behaviour, there are some relative consistencies across the various carnivore species included in this synthesis. First, kill rate studies predominantly report kill rates of ungulates (Fig. 3) because (*i*) they are the primary prey for many large carnivore species globally, (*ii*) the impact of predation on ungulate populations is a hunting and management concern, and (*iii*) sampling methods are biased towards detecting kills of large prey (Mills, 1992; Elbroch, Lowrey & Wittmer, 2018). This means that where large carnivore species co-occur, their selection of ungulate prey often overlaps (Kunkel *et al.*, 1999; Hayward & Kerley, 2008; Wang & Macdonald, 2009). Additionally, there is a close positive relationship between the body mass of most large terrestrial carnivore species and the mass of their main prey (ursids excepted) owing to increasing energy expenditure associated with a larger carnivore body mass and catching and subduing large prey (Carbone *et al.*, 1999; Carbone, Teacher & Rowcliffe, 2007; Radloff & Du Toit, 2004; Tucker, Ord & Rogers, 2016; De Cuyper *et al.*, 2019). Thus, many large terrestrial carnivore species are energetically constrained to catching larger prey, and the mass of a carnivore's main prey generally scales with carnivore mass (Carbone *et al.*, 1999, 2007). For these reasons we provide a comparison of typical kill rates across carnivore species and provide tentative interpretations of observed trends that are supported by previous research. The aggregated kill rates we present here should not be considered a substitute for kill rates determined from robust system-specific studies.

(2) Kill rates for group *versus* solitary carnivores

Kill rates of ungulates (Fig. 3) and ungulate and non-ungulate prey (Fig. 4) for social groups of carnivores are similar to, or higher than, kill rates of solitary carnivores. However, when group kill rates are calculated *per capita* carnivore, brown bears and most solitary felids kill more frequently, on average, than group-living carnivores (Figs 3–5). Lower *per capita* kill rates by group-living carnivores may be indicative of the multiple benefits associated with group foraging such as

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Fig. 2. Distribution of large carnivore kill rate studies according to terrestrial biomes. (A) Location of unique large carnivore kill rate studies according to terrestrial biomes as per Dinerstein *et al.* (2017). (B) Number of unique kill rate studies per species and biome, and indication of whether there were significantly ($p < 0.05$) more (cyan boxes) or less (brown boxes) kill rate studies conducted in certain biomes than would be expected; using Monte Carlo chi-squared goodness-of-fit tests with simulated p-value, we tested whether the number of studies was proportionate to the relative proportion a biome contributed to the global distribution of a species (Tables S9–S25). Light grey boxes indicate instances where the number of kill rate studies per species and biome were not significantly lower than expected, with dark grey boxes highlighting instances where no kill rate studies were located and this was not significant. Numbers in parentheses indicate the proportion (%) that the biome contributes to the global distribution of that species according to IUCN *Red List* species distribution maps (IUCN, 2022) and dingo distribution (Cairns *et al.*, 2018). Biome information was extracted from terrestrial biomes (Dinerstein *et al.*, 2017) using study locations and reported study area size. A biome had to constitute at least 25% of the study area and at least 1% of a species global distribution to be included. Biome information for one jaguar study (Cavalcanti & Gese, 2010) was not included because the study location could not be reliably determined.

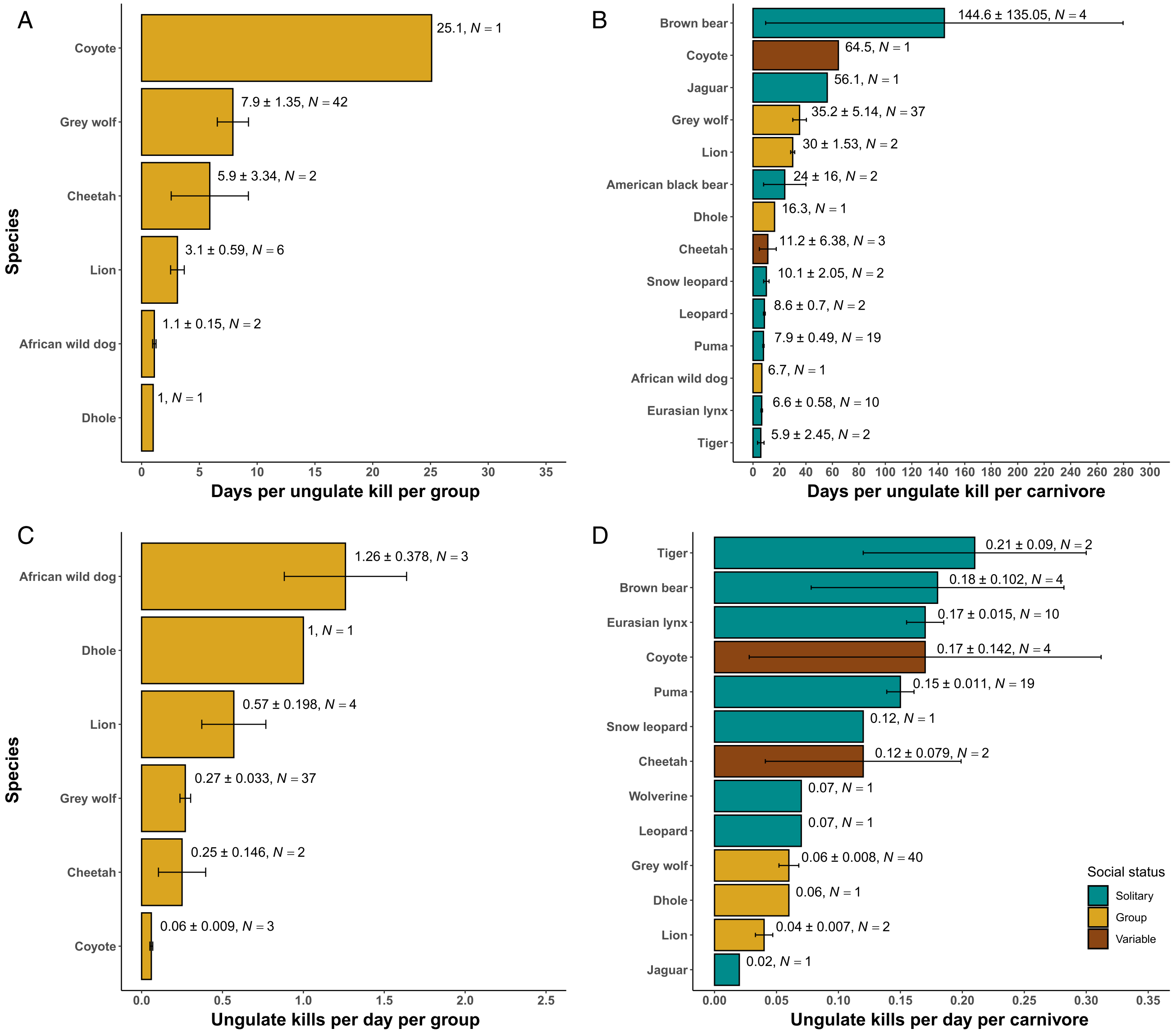


Fig. 3. Mean kill rates calculated and/or standardised from kill rate data reported as ungulates killed per unit of time. Bars represent the mean ± SE ungulate-only kill rate for each large carnivore species and sample size (N) of unique studies contributing an average kill rate estimate to the overall mean kill rate per species. (A) Days per ungulate kill per group of carnivores. (B) Days per ungulate kill per carnivore. (C) Ungulate kills per day per group of carnivores. (D) Ungulate kills per day per carnivore. Key indicates the social status of each carnivore species according to whether they are typically "solitary", typically "group" living, or if they interchangeably occur both as solitary individuals and in groups (i.e. "variable").

access to larger prey and greater hunting success (Kruuk, 1975; Stander, 1992*a*; MacNulty *et al.*, 2014), reduced food losses to scavengers/kleptoparasites (Vucetich, Peterson & Waite, 2004; Smith *et al.*, 2012), higher net energy gains from hunting together (Suter & Houston, 2021), and avoidance of costs and risks of hunting for non-cooperative group members (Packer & Ruttan, 1988). For example, success in killing large dangerous prey such as bison increases with increasing wolf pack size (MacNulty *et al.*, 2014), and coalitions of male cheetahs can kill larger prey and achieve higher *per capita* food acquisition rates compared to solitary cheetahs (Mills, Broomhall & du Toit, 2004). The benefits of sociality may also drive reciprocal social tolerance of conspecifics and sharing of kills by typically "solitary" carnivore species, as it allows them to mitigate energy expenditure associated with foraging, as well as risks associated with hunting and antagonistic interactions (Elbroch *et al.*, 2017*b*). Group living, however, does not always provide greater access to food, hence social carnivores such as lions, wolves, and spotted hyaenas may disassociate and hunt alone, depending on the vulnerability and availability of prey (Kruuk, 1975; Smith *et al.*, 2012;

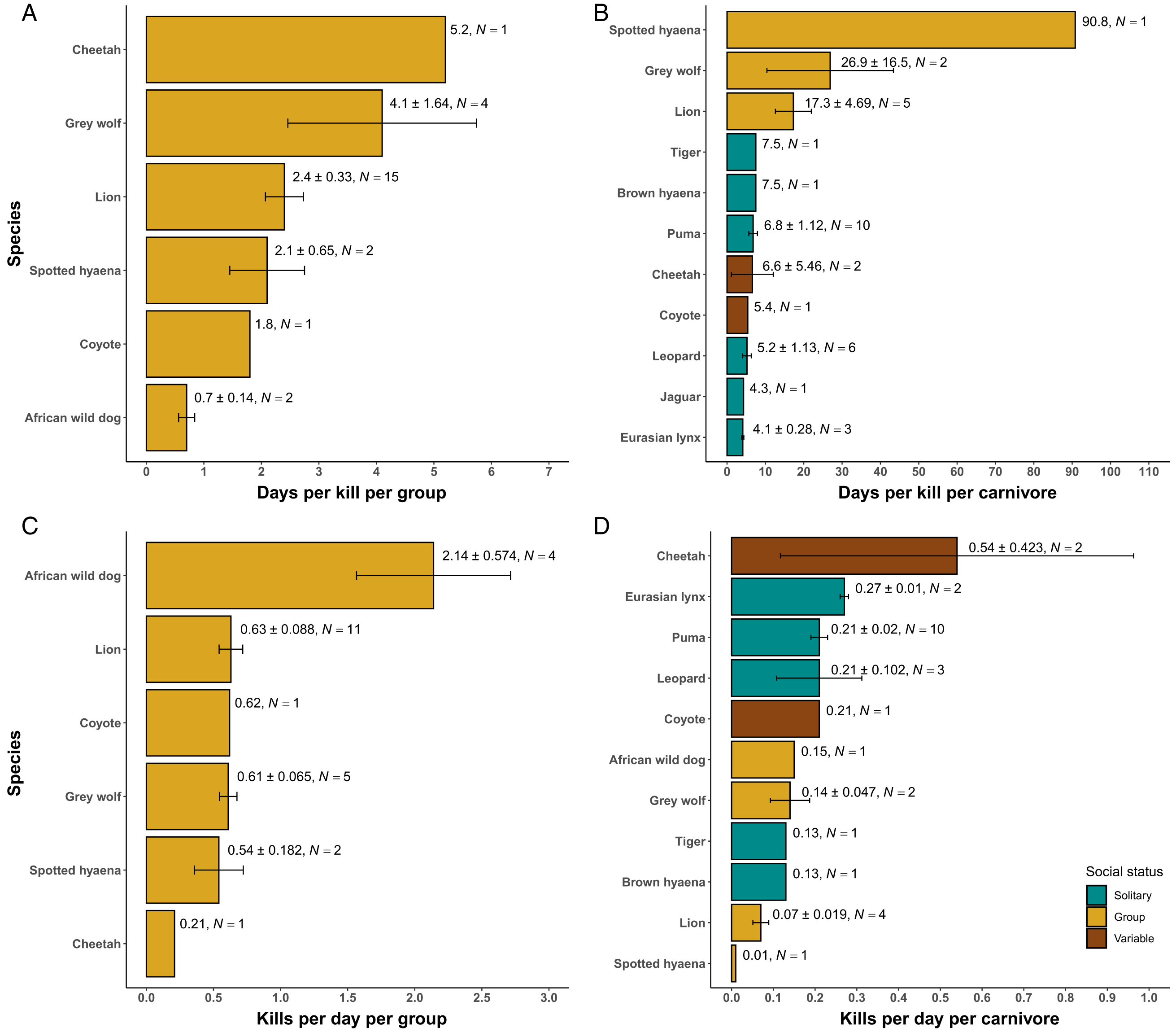


Fig. 4. Mean kill rates calculated and/or standardised from kill rate data for all prey, inclusive of ungulate and non-ungulate prey killed per unit of time (does not include ungulate-exclusive kill rates). Bars represent the mean ± SE kill rate for each large carnivore species and sample size (*N*) of unique studies contributing an average kill rate estimate to the overall mean kill rate per species. (A) Days per kill per group of carnivores. (B) Days per kill per carnivore. (C) Kills per day per group of carnivores. (D) Kills per day per carnivore. Key indicates the social status of each carnivore species according to whether they are typically "solitary", typically "group" living, or if they interchangeably occur both as solitary individuals and in groups (i.e. "variable").

Messier, 1985; Packer, Scheel & Pusey, 1990; Barber-Meyer & Mech, 2015; Gable *et al*., 2016).

Group-living carnivores often exhibit similar or lower *per capita* kill rates of food acquisition compared to multiple solitary carnivore species, despite often having a greater body mass (Fig. 6). This could indicate costs associated with food sharing, whereby each individual has access to less food because of consumption by other group members, or conversely it could indicate a greater ability of social carnivores to defend and consume large prey (Carbone, Du Toit & Gordon, 1997), as compared to solitary carnivores that lose more of their kills to scavengers and kleptoparasites. Beyond cooperative hunting, social carnivores share diverse benefits from cooperative strategies, such as predator avoidance through "dilution" of individual attack, cooperative defence of resources, and shared parenting (Macdonald, 1983; Kitchen & Packer, 1999). By contrast, solitary species make less noise when stalking prey in complex habitats, and avoid potential costs of intraspecific competition, including reduced access to shared resources (Kleiman & Eisenberg, 1973; Bekoff, Daniels & Gittleman, 1984; Caro, 1989).

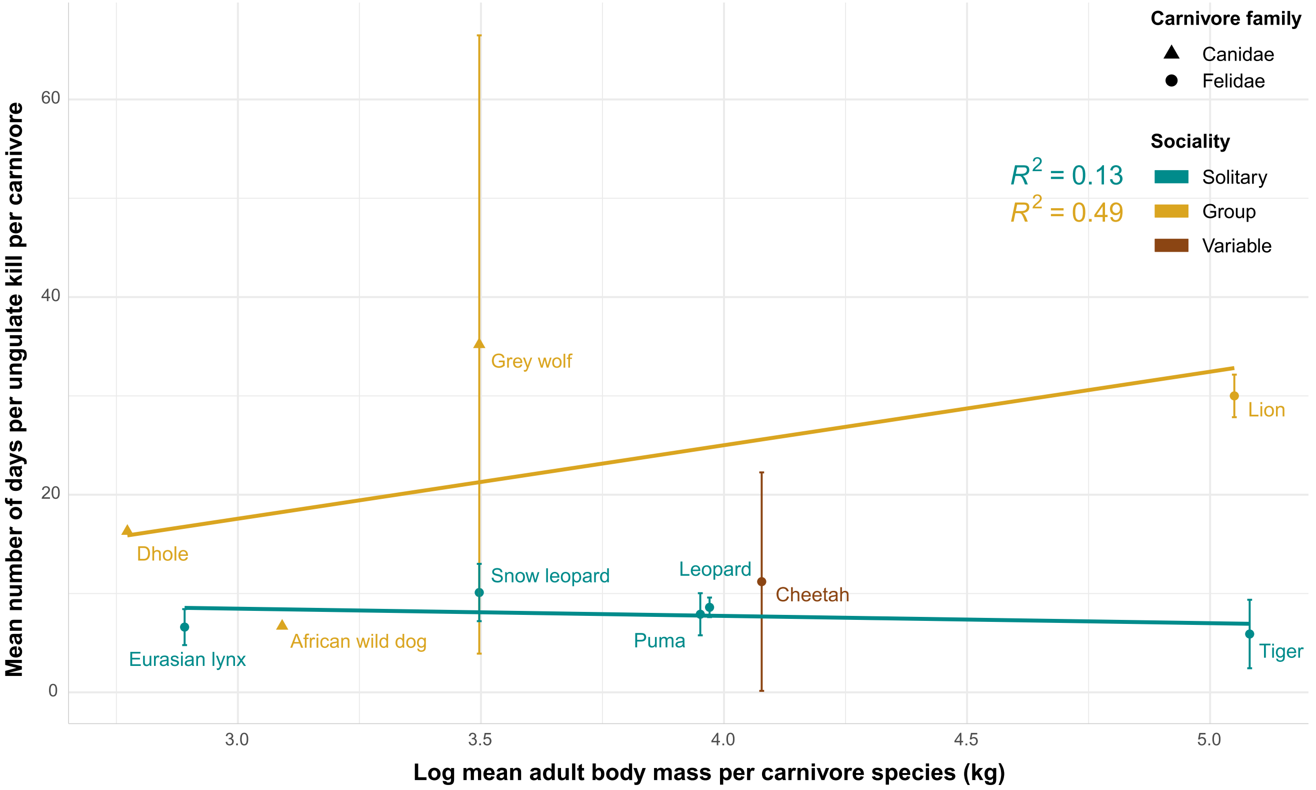


Fig. 5. Mean number of days per ungulate kill per carnivore relative to log mean adult body mass (kg) for carnivore species that predominantly prey on ungulates. Kill rates calculated and/or standardised from kill rate data reported as ungulates killed per unit of time. Vertical error bars (+SE) displayed per species, with data coming from multiple studies. Key indicates carnivore family and sociality according to whether they are typically "solitary", typically "group" living, or if they interchangeably occur both as solitary individuals and in groups (i.e. "variable"). Trendlines and R^2 values displayed according to sociality.

Although based on a limited number of species, our findings indicate that large solitary carnivores that predominantly prey on ungulates (all of which are felids), kill ungulates at similar rates regardless of carnivore body mass (Fig. 5). A close predator to prey size relationship has been identified for many large terrestrial carnivore species (Carbone *et al*., 1999, 2007); research (in a tropical setting) indicates predation efficiency is highest when carnivores target prey approximately equal to their own body mass (Chakrabarti *et al*., 2016). Our findings may be indicative of this relationship, whereby kill rates remained relatively constant across large solitary felid species despite these carnivore body masses ranging by nearly an entire order of magnitude (i.e. Eurasian lynx 18 kg *versus* tiger 161 kg mean adult body mass). This trend has even been observed between sexually dimorphic females and males of the same carnivore species, for example solitary female and male pumas have been found to kill ungulates at similar rates despite males being larger than females, and this could be explained by males killing larger prey (Clark *et al*., 2014). The solitary felids we assessed (Fig. 5) are known to target ungulates whilst opportunistically killing smaller alternative prey species (Hunter & Barrett, 2018), suggesting they employ an optimal foraging strategy that maximises food acquisition relative to energy expenditure associated with hunting (MacArthur & Pianka, 1966; Griffiths, 1980). However, the size of prey selected by large carnivores is also likely constrained by multiple factors, such as carcass utilisation and digestibility (Chakrabarti *et al*., 2016), and risk of injury to the predator while hunting (Hayward *et al*., 2006; Mukherjee & Heithaus, 2013). Furthermore, small and non-ungulate prey species can take on greater importance in the diets of some of these large felids depending on predator age and sex, season (Odden, Linnell & Andersen, 2006; Elbroch, Feltner & Quigley, 2017*a*), prey availability, geographic location (Mengüllüoğlu *et al*., 2018; Gaston *et al*., 2024), and urbanisation (Moss, Alldredge & Pauli, 2016; Smith, Wang & Wilmers, 2016), thus emphasising the need for predation studies across differing contexts.

(3) Kill rates beyond ungulates and obligate carnivores

Whilst non-ungulate prey contributes a comparatively small amount of biomass to the diets of many large carnivore species for which kill rates have been calculated, alternative prey may still be an important food source for some large carnivores. For example, jaguars appear less reliant on ungulate

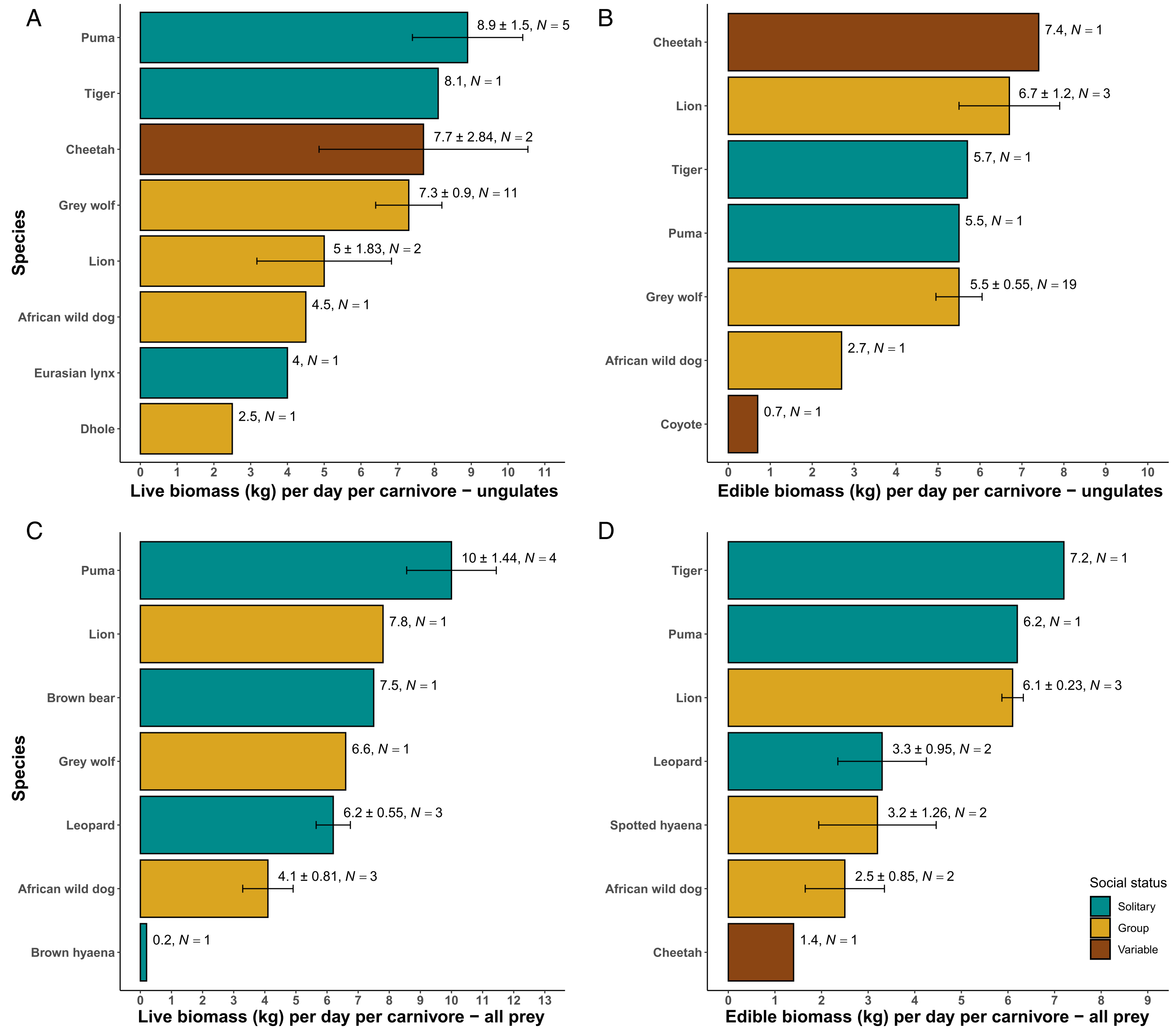


Fig. 6. Mean kill rates calculated from kill rate data reported as biomass in kilograms killed per predator per day. Bars represent the mean ± SE biomass kill rate for each large carnivore species and sample size (N) of unique studies contributing an average kill rate estimate to the overall mean kill rate per species. Live biomass is calculated from the live mass of prey killed and includes non-edible parts, whereas edible biomass excludes the estimated mass of non-edible parts from the live mass of killed prey. "Ungulates" represents kill rates that are exclusively for ungulate prey. "All prey" represents kill rates that include ungulate and non-ungulate prey and does not include ungulate-exclusive kill rates. (A) Ungulate kills – live biomass. (B) Ungulate kills – edible biomass. (C) Ungulate and non-ungulate kills – live biomass. (D) Ungulate and non-ungulate kills – edible biomass. Key indicates the social status of each carnivore species according to whether they are typically "solitary", typically "group" living, or if they interchangeably occur both as solitary individuals and in groups (i.e. "variable").

prey as compared to other large carnivores (Fig. 3D), with ungulates contributing as low as 40 and up to 62% of kills (Cavalcanti & Gese, 2010; Cassaigne *et al.*, 2016). Only when non-ungulate prey species, such as caiman, are included in analyses do jaguar kill rates resemble those of other large solitary carnivores (Fig. 4B). This highlights the utility of kill rate studies to provide insights into the foraging ecology of large carnivores, such as prey selection, but also indicates the importance of considering the potential impacts carnivores may be having on non-ungulate prey species.

Omnivorous carnivores present a particular challenge, making their kill rates difficult to compare with other species. Bears and coyotes (Fig. 3B, D) are proficient hunters of ungulates in some seasons (Huegel & Rongstad, 1985; Brundige, 1993; Patterson & Messier, 2000; Fortin *et al.*, 2013; Ordiz *et al.*, 2020; Twynham *et al.*, 2021). During the ungulate birthing season, bear predation on neonates (Ballard, Spraker & Taylor, 1981; Boertje *et al*., 1988; Ordiz *et al*., 2020; Twynham *et al*., 2021) over short time periods can significantly impact ungulate populations (Ballard, Gardner & Sterling, 1982; Ballard & Larsen, 1987; Larsen, Gauthier & Markel, 1989; van Ballenberghe & Ballard, 1994). For this reason, accounting for predation by omnivores, even if restricted to short periods during the year, is important when determining total ungulate predation within a system containing multiple large carnivore species (Ballard *et al*., 1981; Barber-Meyer, Mech & White, 2008). In addition to direct predation, bears can also have a significant impact on kill rates and food intake of other carnivores by regularly stealing their kills (Allen *et al*., 2021), although the dynamics of this relationship are unclear in some systems (Tallian *et al*., 2017).

(4) Linking kill rates to bioenergetics

Biomass kill rates measuring the live or edible mass of prey killed per unit time are useful for comparing predation across systems, seasons and species, and can help reveal deeper insights into predator–prey interactions (Metz *et al*., 2012; Elbroch *et al*., 2014; Prugh & Sivy, 2020). For example, in North America, grey wolves kill more prey in summer than in winter due to a high abundance of young vulnerable prey (Sand *et al*., 2008; Knamiller, 2011; Metz *et al*., 2012); however, the biomass killed per wolf per day in summer actually decreases because of predation on smaller prey (Knamiller, 2011; Metz *et al*., 2012). By contrast, grey wolf kill and consumption rates in India appear to remain stable across seasons (Jethva & Jhala, 2004), which indicates differing system-specific dynamics.

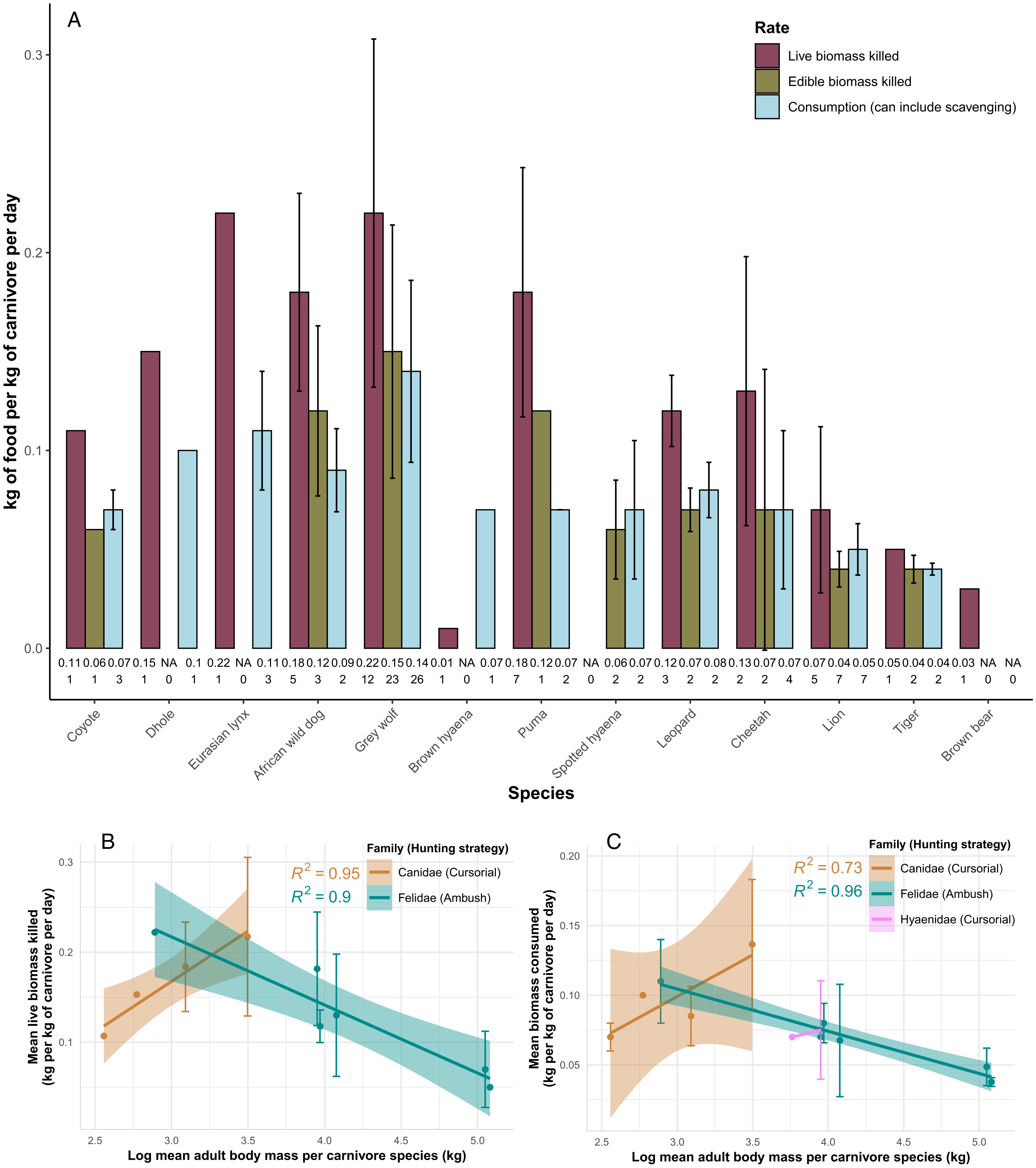
Biomass kill rates can help differentiate between foraging behaviours and other aspects of food acquisition, when the comparison and interpretation of typical kill rates (i.e. measured as the number of prey killed per unit of time) is misleading (see Section VI for recommendations to resolving this). For example, brown hyaenas are reported to kill prey at the same rate as tigers, which are much larger (0.13 kills per day per individual) (Fig. 4B, D); however, when kill rate is calculated as live biomass killed per carnivore, tigers kill ∼41 times more prey biomass per day than brown hyaenas (Fig. 6A, C) (Mills, 1978). This is explained by the fact that brown hyaenas prey predominantly on small mammals and birds, and that kills only represent 5.8% of their dietary biomass. The remainder of brown hyaena diet is composed of carrion and plant foods (Mills, 1978), whereas tigers typically feed on large ungulate prey. This emphasises the importance of measuring and reporting kill rates using multiple metrics as well as reporting raw data from which kill rates are calculated so the relative contribution of different sized prey species can be understood. It also highlights the usefulness of accounting for scavenging to contextualise results and enable appropriate comparisons among species, particularly when feeding ecologies differ considerably.

Carnivores are predicted to exhibit lower kill rates as gut capacity and body mass increases (De Cuyper *et al*., 2019). Our synthesis, however, indicates that physiological factors may also influence kill rates across large carnivore species (Figs 3–7). Members of Canidae show a trend for increasing body mass-standardised biomass kill and consumption rates with increasing body mass (Fig. 7), which is consistent with higher energetic costs associated with a cursorial hunting strategy (i.e. hunts that can be sustained over long distances) as carnivores become larger (Carbone *et al*., 2007). By contrast, members of Felidae demonstrate decreasing body mass-standardised biomass kill and consumption rates with increasing body mass (Fig. 7). This highlights a potential energetic and ecological advantage to ambush hunting (i.e. short and intense hunts often relying on stealth), rather than long hunts, as carnivores increase in size; this pattern might be considered support for Cope's (or Depéret's) rule (Bokma *et al*., 2016; Stanley, 1973).

By linking prey mass to carnivore mass, we can also begin to assess whether carnivores kill more prey than they are able to consume, and if so, the ecological reasons underpinning this discrepancy. When carnivores kill prey larger than they can eat in a single event, for example, they realise a net energy gain (Carbone *et al*., 2007; Rizzuto, Carbone & Pawar, 2018). The limitations imposed by their gut capacity can be overcome by energy-saving strategies that should reduce kill rates, including food caching (Balme *et al*., 2017; van der Veen *et al*., 2020; Allen *et al*., 2023) and defending kills from scavengers (Vucetich *et al*., 2004; Lamprecht, 1981; Cooper, 1991). When these strategies fail, however, loss of food to scavengers, including humans (Sunquist, 1981; Treves & Naughton-Treves, 1999), can reduce consumption rates and increase kill rates of large carnivores (Krofel, Kos & Jerina, 2012; Elbroch *et al*., 2015; Allen *et al*., 2021). For instance, flocks of ravens can remove up to 37 kg of food per day from carcasses and reduce the biomass available to carnivores by 10–66% (Promberger, 1992; Kaczensky, Hayes & Promberger, 2005). Carnivores also can be scavengers and may benefit from other carnivores' kills to reduce their own kill rates. For example, wolverines may reduce their kill rates when sympatric with higher densities of Eurasian lynx because of increased scavenging opportunities (Andrén *et al*., 2011).

Eurasian lynx, African wild dog, puma, and cheetah all kill approximately twice as much, or more, live biomass than they are able to consume (Fig. 7A), and research suggests that large carnivores may abandon, on average, 28% of edible biomass of their kills (Prugh & Sivy, 2020). This behaviour is likely driven by competition with other carnivores, with these species identified as being subjected to, and/or capable of coping with kleptoparasitism by scavengers and competitors (Murphy *et al*., 1998; Gorman *et al*., 1998; Mattisson *et al*., 2011*a*; Krofel *et al*., 2012; Scantlebury *et al*., 2014; Elbroch *et al*., 2015, 2017*c*). For example, research on carrion provisioning by pumas suggests they are abandoning, on average, 50–68% of edible biomass from their kills (Elbroch *et al*., 2014; Barry *et al*., 2019). Researchers have suggested that subordinate large carnivores in particular, such as pumas and cheetahs, may kill more than they consume as a strategy to cope with competition with dominant competitors, such as grey wolves, bears, lions, and hyaenas (Scantlebury *et al.*, 2014; Elbroch *et al.*, 2017*c*). Our analyses estimated the four highest kill rates in terms of number of all prey (ungulates and non-ungulates) per day per carnivore were exhibited by subordinate apex felids (Fig. 4D). In the case of African wild dogs, they occur at lower population densities in areas where the risk of kleptoparasitism by dominant competitors is high (Gorman *et al.*, 1998).

By supplying carrion to their ecosystems, large carnivores facilitate diverse trophic interactions that may foster



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ecological complexity and resilience within biological communities (Wilmers *et al.*, 2003; Mattisson *et al.*, 2011*a*; Prugh & Sivy, 2020). Pumas, for example are estimated to provide more than 1.5 million kilograms of carrion per day to ecological communities across North and South America (Elbroch *et al.*, 2017*c*). These food subsidies have been shown to benefit communities of scavengers including invertebrates (Barry *et al.*, 2019), birds (Elbroch & Wittmer, 2012), small carnivores, and dominant competitors (Murphy *et al.*, 1998; Allen *et al.*, 2015*b*). Subsequently, pumas are considered important ecological brokers of nutrients and energy within their respective ecosystems, thus linking multiple taxa and trophic levels (LaBarge *et al.*, 2022). However, this relationship may be more complex than first thought, and mesocarnivores utilising carrion at larger carnivore kills may experience higher risk of predation and an ecological trap that could suppress mesocarnivore abundance (Prugh & Sivy, 2020).

Body mass-standardised biomass kill rates are not regularly reported in the kill rate literature, yet they provide a useful metric to assess differences in foraging strategies and energetic requirements, as well as community relationships, and ecosystem carrying capacity of carnivores. When coupled with consumption rates these measures provide even greater insight into interspecific relationships, comparative metabolic needs, and population dynamics, because it is consumption rate that may ultimately determine carnivore fitness (Mech, 1977; Bjorge & Gunson, 1989; Miller *et al.*, 2014). Furthermore, variability among species-specific kill rate estimates (Figs 3–7; Data S1 and S2) emphasises the importance of calculating system-specific kill rates across meaningful lengths of time, whilst accounting for multiple influencing factors, to gain a robust understanding of predation dynamics.

IV. IMPLICATIONS OF KILL RATE RESEARCH FOR UNGULATE CONSERVATION AND MANAGEMENT

Competition between carnivores and humans for ungulate meat is an important conservation and management issue (Berger, 2005) that appears to have driven most kill rate research. For example, kill rates are widely used in the management of North American ungulate populations where the emphasis of kill rate research is on grey wolves and pumas. State management agencies use statistical models to calculate ungulate abundance before setting annual hunting quotas and issuing hunting permits/tags. Therefore, game managers need to know how many ungulates they should expect to lose to predators before setting sustainable quotas. Additionally, ungulate (including livestock) and carnivore management has typically focused on increasing ungulate harvests by improving habitat quality and foraging opportunities for ungulates, or by reducing the number of carnivores that might hunt these same ungulates (Ballard *et al.*, 1987; Gasaway *et al.*, 1992; Treves & Naughton-Treves, 1999; Andrén *et al.*, 2006; Schmidt, Burch & MacCluskie, 2017; DeCesare *et al.*, 2018; Miller, Person & Bowyer, 2022).

Research informed by large carnivore kill rates has often been used to emphasise the impacts of carnivores on prey species that humans value (Okarma *et al.*, 1997; Hayes & Harestad, 2000; Vucetich *et al.*, 2011; Mattisson *et al.*, 2014). Despite an often limited set of motivations, kill rate studies have contributed to our understanding of the broad ecological roles performed by large carnivores and their impacts on ungulate prey (Messier & Crête, 1985; Okarma *et al.*, 1997; Hayes & Harestad, 2000; Power, 2002), predator–prey dynamics (Nilsen *et al.*, 2009; Vucetich *et al.*, 2011), carnivore foraging requirements (Schaller, 1976; Mech, 1977), prey selection (Elbroch *et al.*, 2013; Sand *et al.*, 2016), and other carnivore foraging phenomena (MacNulty *et al.*, 2009; Elbroch & Wittmer, 2013; Tallian *et al.*, 2017). Kill rate-informed research has also indicated the potential benefits carnivores provide to humans by acting as biological controls that suppress the impacts of herbivores (Prowse *et al.*, 2015), indirectly mitigating deer–vehicle collisions (Gilbert *et al.*, 2017; Raynor, Grainger & Parker, 2021), management of non-native species (Braczkowski *et al.*, 2018; Andreasen *et al.*, 2021), and potentially reducing risk of disease transmission (Braczkowski *et al.*, 2018). Further, kill rates have been used to highlight the ecological contributions of carnivores to energy pathways and nutrient cycling that support biodiversity and ecological resilience

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Fig. 7. Body mass-standardised biomass kill rates and relationship with hunting strategy and carnivore family. (A) Mean ± SD biomass kill and consumption rates reported as kilograms of prey per kilogram of carnivore per day (see Data S2). Sample size of unique studies contributing an average estimate to the overall mean rate per species is displayed along the *x*-axis. "Live" biomass, calculated from the live mass of prey killed, includes non-edible parts, "Edible" biomass excludes estimated mass of non-edible parts from live mass of killed prey, and "Consumption" includes killed and scavenged prey (excluding uneaten portions). "Live" biomass kill rate for coyote is for non-ungulate prey only. "Consumption" rate for brown hyaena includes non-animal foods. Species ordered from left to right according to average body mass (range = 12.9–161 kg). (B) Relationship between hunting strategy and the mean ± SD body mass-standardised live biomass kill rate of ungulate and non-ungulate prey per carnivore species, measured as kg of live prey biomass killed per kg of carnivore per day. Trendline is shown with 95% confidence interval (CI, shaded) and R^2 value. Brown hyaena and brown bear were not included because their hunting behaviour is considerably different. (C) Relationship between taxonomic family and the mean ± SD body mass-standardised consumption rate of ungulate and non-ungulate prey per carnivore species, measured as kg of killed and scavenged prey biomass per kg of carnivore per day (excludes uneaten portions of kills). Trendline is shown with 95% CI and R^2 value.

(Peziol *et al.*, 2023), and the suppression of mesocarnivores (Prugh & Sivy, 2020). Despite the benefits large carnivores provide, they may continue to be persecuted because of their perceived or actual threat to livestock, wild ungulates, and humans, and a lack of appropriate research to confirm or challenge standing perceptions (Treves, 2009; Rode *et al.*, 2021; Elbroch & Treves, 2023) or appropriate management actions (Treves, Krofel & McManus, 2016; Miller *et al.*, 2022). This is the case for dingoes in Australia (van Eeden *et al.*, 2021), for which no reliable kill rate estimates exist.

Kill rate studies rarely account for the complexity of predation within a community-level framework as they typically focus on a single carnivore species and determine kill rate estimates only for ungulate prey. This provides a limited perspective from which to draw conclusions, meaning even well-intentioned management actions may result in unexpected and undesirable consequences for species and ecosystems that could possibly have been averted if appropriate predation studies accounting for system complexity were first undertaken (Wittmer *et al.*, 2013; Keehner, Wielgus & Keehner, 2015).

It is important to note that carnivore kill rates in isolation do not allow us to understand predation impacts on prey populations unless accompanied by prey density (i.e. "functional response") and subsequent change in carnivore density (i.e. "numerical response"), to measure total predation (Holling, 1959). For example, one can integrate kill rate data to measure the proportion of the prey population removed by predators per unit of time ("predation rate") (Vucetich *et al.*, 2011; Metz *et al.*, 2020; Støen *et al.*, 2022), or to calculate mortality rates due to predation to compare with other cause-specific mortality rates (Ballard, Miller & Whitman, 1990; Okarma *et al.*, 1997) to determine whether predation is additive or compensatory (Krebs *et al.*, 1995; Sand *et al.*, 2012*b*). Additionally, alternative methods for measuring predation impacts on prey populations exist and can be used in place of, or in conjunction with, kill rate studies. For example, causes of mortality, including predation attributable to each predator species, can be measured by exclusively monitoring prey populations. However, similar to kill rates being focused on the predator, this approach focuses on just the prey and provides no information on the individual foraging requirements of the predators. Thus, integrated approaches of monitoring both predators and prey offer the most comprehensive insight into predator–prey dynamics (e.g. Støen *et al.*, 2022).

V. KILL RATES CAN AID OUR UNDERSTANDING OF GLOBAL CHANGE

Human activities have led to the decline and loss of large carnivores in various regions globally, resulting in significant changes to the functional roles performed by large carnivores, and associated community dynamics (Estes *et al.*, 2011; Ripple *et al.*, 2014; Kuijper *et al.*, 2016). Kill rates provide a tractable, repeatable metric that can be used for assessing and comparing the extent and severity of human impacts on large carnivore foraging behaviour and trophic relationships across ecosystems. Despite the importance of kill rates in understanding predator–prey interactions, their utility is not widely recognised, and insufficient research limits our ability fully to appreciate and predict the consequences of modified predation regimes (Kuijper *et al.*, 2016), justify current management actions affecting carnivores (Treves, 2009; Eklund *et al.*, 2017; Miller *et al.*, 2022), or inform effective conservation measures. Thus, evidenced-based carnivore management and conflict mitigation is critical for avoiding further disruption and breakdown of ecosystem functioning, environmental decline, and biodiversity loss (Estes *et al.*, 2011; Ripple *et al.*, 2014; Plumptre *et al.*, 2021).

Our current understanding of the impact of human activities such as habitat destruction and modification, direct persecution, climate change, and other threats on large carnivore kill rates is severely lacking and risks poor outcomes for carnivores, their prey and ecosystem processes more broadly. Only one study has explicitly examined the connection between human activities and kill rates (Smith *et al.*, 2015). This study found that female pumas in areas with high housing density decreased the time they spent consuming deer and compensated for this by increasing their kill rates (Smith *et al.*, 2015). Other studies have linked human disturbance to potential impacts on large carnivore kill rates without explicitly exploring this relationship, and these have predominantly focused on grey wolves (Fuller & Keith, 1980; Sand *et al.*, 2012*a*; Zimmermann *et al.*, 2015; Benson *et al.*, 2017).

Predicting and responding to the effects of global human-induced climate change on species and ecological communities presents a significant challenge to ecologists and relies on understanding its direct and indirect effects (Gilman *et al.*, 2010). Climate change may disrupt established patterns of synchrony, such as food requirements, food availability and reproduction, and subsequently modify species interactions and impact community stability (Gilman *et al.*, 2010), particularly in environments where synchrony is an adaptation to climatic seasonality (Durant *et al.*, 2007). Therefore, understanding how species interact, including predators and their prey, may be important for understanding the potential impacts of climate change (Åkesson *et al.*, 2021).

Climate change is predicted to impact large carnivores negatively through multiple pathways, including elevated conflict with humans (Helman, Zarzo Arias & Penteriani, 2022) and altered predator behaviour, perhaps leading to trophic cascades (Post *et al.*, 1999). Moreover, climate change is leading to increased temperatures and altering seasonal climatic conditions, which has implications for ecological processes (Walther *et al.*, 2002), including predator–prey dynamics (Post *et al.*, 1999; Nilsen *et al.*, 2009; Bastille-Rousseau *et al.*, 2018; Peers *et al.*, 2020), predator–scavenger interactions (Wilmers & Post, 2006), and kill rates (Rall *et al.*, 2012). Patterns of predation and kill rates can vary

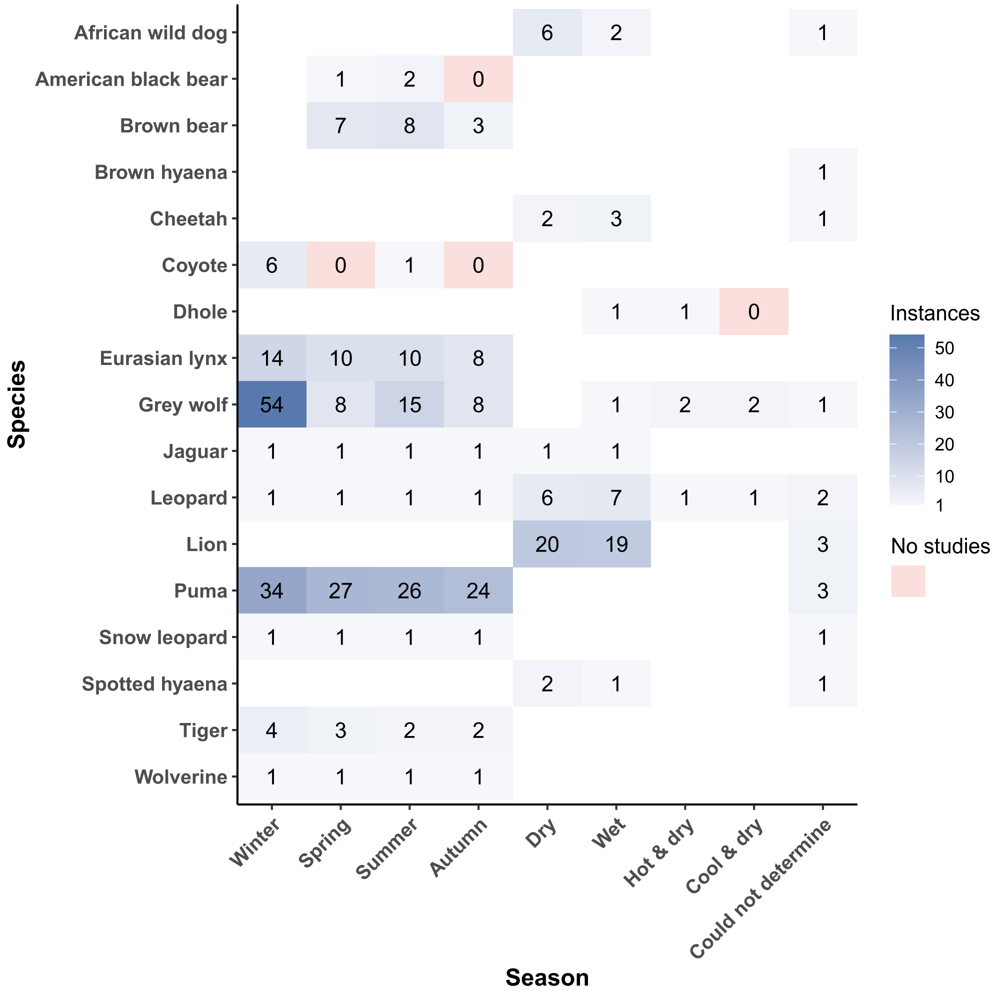

Fig. 8. Number of unique kill rate studies that met our inclusion criteria per species per season in which kill rate data was collected and reported. Blank cells indicate that the season description is not applicable to the location where studies have been conducted, or the study seasons could not be determined for that study. Kill rates were not necessarily reported for each season but sampling occurred across these seasons.

markedly among seasons, mostly due to prey vulnerability (Nilsen *et al.*, 2009; Metz *et al.*, 2012; Ordiz *et al.*, 2020), which can be influenced by abiotic factors such as snow depth (Nilsen *et al.*, 2009). By monitoring kill rates across extended periods of time, calculating seasonal kill rates, and integrating this information with changes in prey abundance and even the plant community, the community-level impacts of changing climatic conditions can be interrogated (Post *et al.*, 1999). Large carnivore kill rates may also be useful for predicting ecosystem resiliency in response to climate change (Wilmers & Post, 2006; Wilmers, Post & Hastings, 2007).

For most large carnivore species, kill rate studies have been conducted across multiple seasons, however the total number of studies remains limited for most species (Fig. 8). Additionally, seasonal kill rates are not always calculated and reported, which could reduce our ability to predict the potential effects of climate change on predator–prey dynamics and ecological systems. Despite being the best-represented species among the kill rate literature, most kill rate research for grey wolves has been conducted during winter, which restricts our understanding of their predatory behaviours during other seasons (Fig. 8) and may impair our ability to assess potential climate change impacts for even well-studied large carnivore species.

VI. CONCLUSIONS

(1) Kill rates provide crucial insights into complex ecological and conservation conundrums, and yet our review highlights how rarely they have been calculated for most of the world's large carnivores. Instead, most kill rate research appears to have been motivated by a narrow set of management objectives concerning human–carnivore conflict for ungulates; potentially limiting current understanding of the functional role of many carnivore species. We advocate for future kill rate studies that address the gaps we have identified, in terms of

particular species and under-represented biomes and geographies. Further, we encourage research to understand the influence of human activities and climate change on carnivore kill rates to inform appropriate conservation strategies for ecosystems and human society. This work would complement the extensive literature examining other facets of large carnivore predation that was beyond the scope of this review, which also provides critical insights into carnivore ecology and predation impacts and is equally important for the conservation and management of carnivores and their ecosystems.

(2) Our analysis of kill rates provides valuable insights into the ecology and functional dynamics of large carnivores. Our synthesis has shown that group-living large carnivore species generally have lower *per capita* kill rates than solitary species, which could indicate advantages associated with group living. Additionally, body mass-standardised kill and consumption rates for Canidae correlate positively with body mass, reflecting energy costs associated with cursorial hunting, while ambush predators show an opposing trend, suggesting potential energetic advantages of ambush hunting with increasing body mass. Furthermore, our findings highlight the crucial role of subordinate carnivores in nutrient cycling by provisioning food to other trophic levels within ecosystems.

(3) Kill rates are useful for understanding carnivore foraging needs but to understand the impact of predation on biological communities, additional data needs to be collected. Thus, we emphasise the need for undertaking kill rate research within a community framework that accounts for system complexity (Nilsen *et al.*, 2009; Estes *et al.*, 2011; Wittmer *et al.*, 2013; Ripple *et al.*, 2014; Elbroch *et al.*, 2015, 2017*c*; Chan *et al.*, 2017; Tallian *et al.*, 2017; Bastille-Rousseau *et al.*, 2018; Prugh & Sivy, 2020). Ideally, this research would include (*i*) the kill and consumption rates, both numerical and biomass, for all large and meso-carnivore species in a system across all prey species, (*ii*) abundance and mortality rates of prey populations, including alternate prey, and (*iii*) carnivore abundance, both of the predator and competitors, and carnivore fitness metrics over time. Studies of this magnitude will no doubt be difficult and require considerable resources to undertake. Comprehensive research of this nature will help to identify the mechanisms driving predator–prey interactions and the impact of carnivores on prey populations and ecosystems more broadly. Such research endeavours should be increasingly sought if we are to understand and respond adequately to the impacts of global change.

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VIII. AUTHOR CONTRIBUTIONS

Conceptualisation: H.U.W., L.M.E., L.D.E., E.G.R., D.W.; Methodology: L.D.E., H.U.W., L.M.E., D.W., E.G.R.; Investigation: L.D.E., K.K., K.J.B., J.J.P.; Formal analysis: L.D.E.; Data curation: L.D.E.; Visualisation: L.D.E.; Funding acquisition: L.D.E., E.G.R., D.W.; Project administration: L.D.E., H.U.W., E.G.R.; Supervision: H.U.W., L.M.E., E.G.R., D.W., L.D.E.; Writing – original draft: L.D.E., H.U.W., L.M.E.; Writing – review & editing: L.D.E., H.U.W., L.M.E., E.G.R., D.W., K.K., K.J.B., J.J.P. The authors declare that they have no competing interests.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Methodology for approach to review including search terms, screening process, data extraction, synthesis and list of included papers, as well as statistical analyses.

Fig. S1. Flow diagram detailing the number of studies identified, screened/reviewed, excluded and included at each stage of the systematic review process, and the respective data sources.

Table S1. Counts and proportions of studies relative to continent.
Table S2. Counts and proportions of studies relative to country.
Table S3. Counts and proportions of studies relative to species and continent.
Table S4. Counts and proportions of studies relative to species and country.
Table S5. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent – observed counts weighted by number of large carnivore species occurring per continent.
Table S6. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent – unweighted counts.
Table S7. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome – observed counts weighted by number of large carnivore species occurring per biome.
Table S8. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome – unweighted counts.
Fig. S2. Individual carnivore species extant ranges indicated in blue, with unique kill rate study locations indicated by black circles.
Table S9. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – African wild dog.
Table S10. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – American black bear.
Table S11. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Brown bear.
Table S12. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Brown hyaena.
Table S13. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Cheetah.
Table S14. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Coyote.
Table S15. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Dhole.
Table S16. Monte Carlo chi-square goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Eurasian lynx.
Table S17. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Grey wolf.
Table S18. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Jaguar.
Table S19. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Leopard.
Table S20. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Lion.
Table S21. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Puma.
Table S22. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Snow leopard.
Table S23. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Spotted hyaena.
Table S24. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Tiger.
Table S25. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by biome with expected counts weighted by biome percentage contributing to species global distribution – Wolverine.
Table S26. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent and species – Africa.
Table S27. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent and species – Asia.
Table S28. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent and species – Europe.
Table S29. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent and species – North America.
Table S30. Monte Carlo chi-squared goodness-of-fit test for kill rate studies by continent and species – South America.
Table S31. Monte Carlo chi-squared goodness-of-fit test only for species with kill rate studies.
Table S32. Monte Carlo chi-squared goodness-of-fit test for all species, including those without any kill rate studies.
Data S1. Data extracted from included papers.
Data S2. Body mass-standardised kill and consumption rates.

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