Topcats and underdogs: intraguild interactions among three apex carnivores across Asia's forestscapes

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ABSTRACT

Intraguild interactions among carnivores have long held the fascination of ecologists. Ranging from competition to facilitation and coexistence, these interactions and their complex interplay influence everything from species persistence to ecosystem functioning. Yet, the patterns and pathways of such interactions are far from understood in tropical forest systems, particularly across countries in the Global South. Here, we examined the determinants and consequences of competitive interactions between dholes *Cuon alpinus* and the two large felids (leopards *Panthera pardus* and tigers *Panthera tigris*) with which they most commonly co-occur across Asia. Using a combination of traditional and novel data sources ($N = 118$), we integrate information from spatial, temporal, and dietary niche dimensions. These three species have faced catastrophic declines in their extent of co-occurrence over the past century; most of their source populations are now confined to Protected Areas. Analysis of dyadic interactions between species pairs showed a clear social hierarchy. Tigers were dominant over dholes, although pack strength in dholes helped ameliorate some of these effects; leopards were subordinate to dholes. Population-level spatio-temporal interactions assessed at 25 locations across Asia did not show a clear pattern of overlap or avoidance between species pairs. Diet-profile assessments indicated that wild ungulate biomass consumption by tigers was highest, while leopards consumed more primate and livestock prey as compared to their co-predators. In terms of prey offtake (ratio of wild prey biomass consumed to biomass available), the three species together harvested 0.4–30.2% of available prey, with the highest offtake recorded from the location where the carnivores reach very high densities. When re-examined in the context of prey availability and offtake, locations with low wild prey availability showed spatial avoidance and temporal overlap among the carnivore pairs, and locations with high wild prey availability showed spatial overlap and temporal segregation. Based on these observations, we make predictions for 40 Protected Areas in India where temporally synchronous estimates of predator and prey densities are available. We expect that low prey availability will lead to higher competition, and in extreme cases, to the complete exclusion of one or more species. In Protected Areas with high prey availability, we expect intraguild coexistence and conspecific competition among carnivores, with spill-over to forest-edge habitats and subsequent prey-switching to livestock. We stress that dhole–leopard–tiger co-occurrence across their range is facilitated through an intricate yet fragile balance between prey availability, and intraguild and conspecific competition. Data gaps and limitations notwithstanding, our study shows how insights from fundamental ecology can be of immense utility for applied aspects like large predator conservation and management of human–carnivore interactions. Our findings also highlight potential avenues for future research on tropical carnivores that can broaden current understanding of intraguild competition in forest systems of Asia and beyond.

Key words: carnivore sympatry, *Cuon alpinus*, intraguild interactions, niche partitioning, *Panthera tigris*, *Panthera pardus*, prey biomass, Protected Areas, tropical ecosystems.

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I. INTRODUCTION

Our understanding of interspecific competition has a long history (Grinnell, 1917; Elton, 1927; Hutchinson, 1957; Macarthur, 1965). Yet, studies continue to generate hitherto unknown or under-appreciated patterns and pathways of species interactions, both in terms of competition theory (e.g. Amarasekare, 2010) and empirical assessments (e.g. Turcotte & Levine, 2016). Recent work has shown how competitive interactions can match or even supersede other ecological attributes to drive distributions and range limits of entire communities (Freeman, Strimas-Mackey & Miller, 2022). Mechanisms that broadly fit the term 'competitive interactions', i.e. interference, exploitation, facilitation, exclusion, can have both proximate and long-term consequences for species and ecological communities (Davis et al., 2017; Braz et al., 2020; Naikatini et al., 2022). At evolutionary timescales, competition can also lead to ecological character displacement, whereby co-occurring competing species show morphological, physiological and behavioural divergence (Grant & Grant, 2006). Depending on the geographic and ecological contexts within which they co-occur, species can display a range of nuanced adaptations (functional traits, sociality, etc.) that enable coexistence (Lamprecht, 1981; Persson, 1985). Global changes in the Anthropocene continue to alter competitive interactions and coexistence, rendering these aspects particularly relevant for further scientific investigations.

The critical role of mammalian carnivores in shaping and maintaining terrestrial food webs is widely acknowledged (Terborgh et al., 2001; Ripple et al., 2014). The interactions between carnivores themselves, direct or indirect, have profound consequences for co-predators, meso-carnivores, and other linked species across trophic levels (Ritchie & Johnson, 2009; Vanak et al., 2013; Swanson et al., 2014, 2016). Interference competition is known to structure large carnivore guilds through direct aggressive encounters (Creel & Creel, 1996; Prugh et al., 2009) or behavioural avoidance, typically through spatial and/or temporal segregation as well as dietary partitioning (Durant, 1998; Périquet, Fritz & Revilla, 2015). Avoidance mechanisms such as restricting activities to safe areas or temporal activity shifts can result in loss of access to prey, water and refugia, and consequently alter the fitness and demography of co-predators (Hunter, Durant & Caro, 2007; Dröge et al., 2017; Shores et al., 2019). Given the wide spatial overlaps between large carnivore distributions and human-use areas worldwide, anthropogenic activities can further alter these interactions (see Schuette et al., 2013). In fact, human-induced factors can sometimes overwhelm intraguild interactions, where the carnivores' responses to each other are completely masked by their responses towards anthropogenic impacts (Gompper et al., 2016).

The literature on intraguild interactions in mammalian carnivores is geographically biased towards Africa, North America and Europe (see Prugh & Sivy, 2020). Africa's open savanna habitats offer ample opportunity for visual observations of species interactions, and have served as 'natural laboratories' where ecological hypotheses can be generated and tested (Durant, 1998; Creel, 2001; Broekhuis et al., 2013). Such studies have contributed substantially towards our

understanding of competition-driven population- and community-level processes (Burton *et al.*, 2012; Vanak *et al.*, 2013; Searle *et al.*, 2021). Europe and North America have benefitted from decades of systematic, quantitative studies (Fedriani *et al.*, 2000; Berger, Gese & Berger, 2008). Greater access to financial resources and institutional infrastructure has enabled researchers to pioneer approaches like satellite telemetry and molecular/genetic methodologies to generate large data sets and broaden the frontiers of competition theory (see Ruprecht *et al.*, 2021). Beyond basic assessments of niche segregation, studies focused on temperate forest systems in these continents have revealed mechanisms of multi-species relationships across trophic tiers (e.g. Berger *et al.*, 2008), and nuances like sex-specific responses to intraguild competition (e.g. Grassel, Rachlow & Williams, 2015). Similar endeavours in tropical forest systems, particularly in countries in the Global South, have been far more limited. This may be attributed to the shorter history of systematic research in these countries (Srivathsa *et al.*, 2022), and the difficulties of conducting observational studies in dense habitats. Hypothesis-driven quantitative research on large carnivore competition in tropical forests has only recently begun to gain momentum (De Oliveria & Pereira, 2013; Rayan & Linkie, 2016; Santos *et al.*, 2019; Widodo *et al.*, 2022).

In forest ecosystems of Asia, dholes *Cuon alpinus*, leopards *Panthera pardus*, and tigers *Panthera tigris* (Fig. 1) constitute a triad of sympatric apex predators that occupy the top-most tier across food webs (Ripple *et al.*, 2014). Understanding competitive interactions among these three species has long been of interest to carnivore ecologists (Venkataraman, 1995; Karanth & Sunquist, 1995, 2000). The dhole, in particular, presents an interesting case study; a species that would otherwise be a meso-predator (see Roemer, Gompper & van Valkenburgh, 2009), competes with the two large felids for the apex position, perhaps aided by its gregarious habits and sociality. Because of the constraints associated with studying elusive carnivores in tropical forest habitats, most published studies examining dhole–leopard–tiger interactions involve diet assessments or incidental natural history observations (Srivathsa *et al.*, 2020c). More recently, the widespread application of camera-trapping methodology has allowed quantification of spatio-temporal overlap and avoidance as indicators of competition-driven resource partitioning (e.g. Steinmetz, Seuaturien & Chutipong, 2013; Karanth *et al.*, 2017). Given the wide spectrum of contexts where the three species co-occur, these interactions likely show geographic variations and a complex interplay of predators, prey, space, time, and populations. Yet, there is no comprehensive study that has synthesised all the available information to draw macro-ecological inferences or generate testable predictions.

Focusing on the dhole, we conducted a review and comparative analysis of studies examining its interactions with
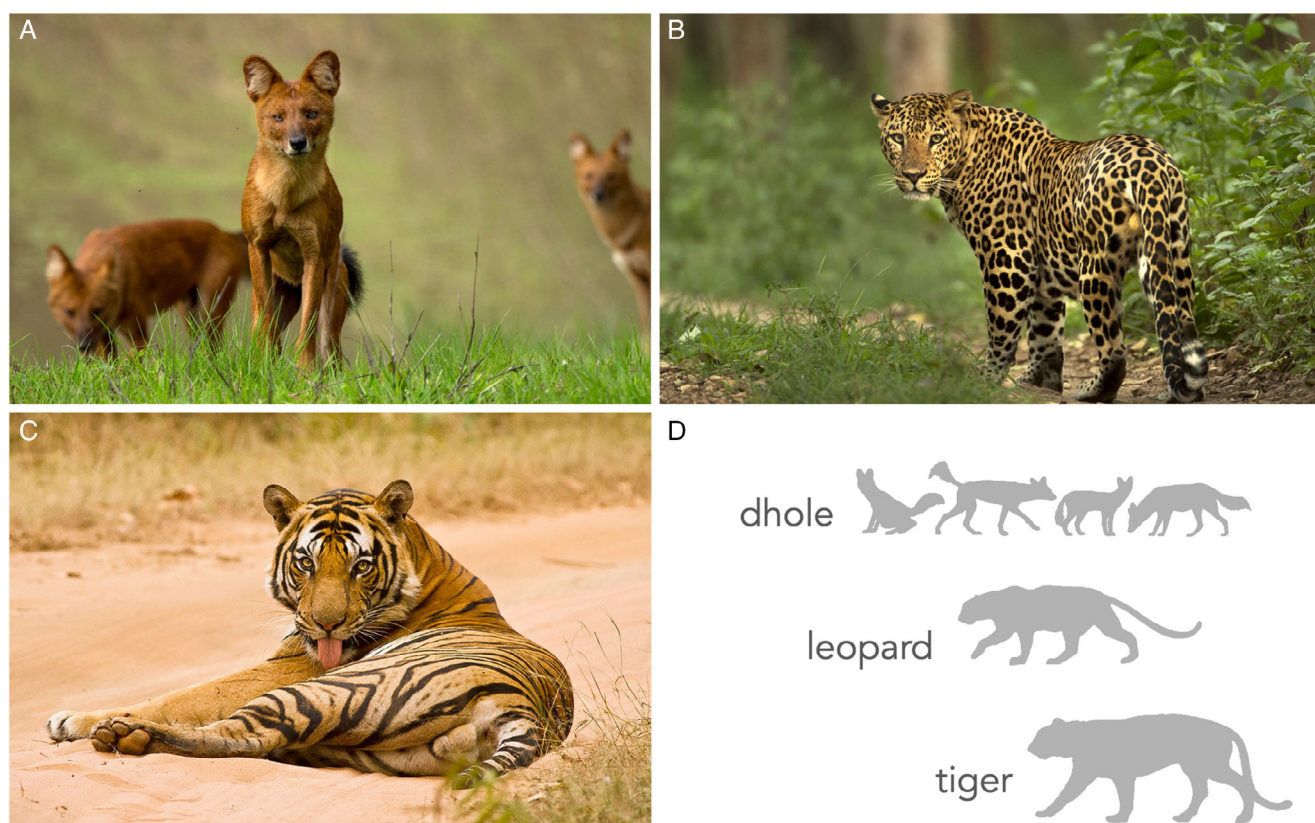
Fig. 1. (A) Dhole (photograph: Sushvin Gowda); (B) leopard (photograph: Kalyan Varma); (C) tiger (photograph: Tamanud Mitra). (D) Icons used to represent the three carnivores in subsequent figures.

leopards and tigers across Asia. Using a range of data sources, we elicited and integrated information from (*i*) rangewide distribution overlaps, (*ii*) direct pairwise interactions, (*iii*) population-level interactions in space and time, (*iv*) diet profiles and overlaps, (*v*) prey availability *versus* offtake, and (*vi*) links between dietary, spatial and temporal niches, to understand the patterns and mechanisms that facilitate or impede sympatry among the three carnivores. Based on these insights, we make predictions for other locations where the strength of intraguild competition can be empirically tested, and discuss the consequences of these results for human–carnivore interactions and large carnivore conservation in Asia's forestscapes.

II. DATA SOURCES AND COLLECTION PROTOCOL

Information on rangewide distributions of the three species was sourced from IUCN; this included predicted historical distribution in 1900 and the most recent distribution assessments from 2020. For the purposes of this study, we used the dhole as a 'fulcrum' to understand interactions among the three carnivores. All our assessments pertain to interactions between two species pairs, dhole–leopard and dhole–tiger, in locations where all three species co-occur. For information on direct pairwise interactions, we first searched *Google Scholar* (www.scholar.google.com) for published literature (searches performed January–July 2022). We focused on locating journal articles, books, natural history notes, etc., in English, using the search terms 'dhole/wild dog', 'leopard', 'tiger', and the respective plural forms and scientific names, without limiting the search to any year or geographic area. We also sourced texts cited within the identified journal articles and books to locate other sources of information. These records were complemented with documented instances of dhole–leopard and dhole–tiger interactions from social media (Facebook, Twitter, Instagram, YouTube), web-based photo-repositories (Flickr, IndiaNatureWatch), online blog articles with photo/video evidence, and nature-based documentary films. The process of finding and collating information from these sources adhered to the protocols outlined in Srivathsa *et al.* (2020*a*). Since their study focused solely on India, their search terms included individual state names and the word 'India', and they targeted country-specific social media groups [see Srivathsa *et al.* (2020*a*) for details]. We did not impose the same restrictions in our search terms or target groups. In all other aspects, we followed the same protocols.

Data on population-level interactions were sourced exclusively from published literature. Using *Google Scholar*, we combined the aforementioned search terms with 'spatial', 'temporal', 'spatio-temporal', 'overlap', 'avoidance', 'sympatry', 'competition' and 'co-occurrence'. Articles located in this manner generally included studies based on camera-trapping surveys. To examine and analyse diet profiles, overlaps, prey availability and offtake, we used a recent meta-analysis of rangewide dhole diet patterns (Srivathsa, Sharma & Oli, 2020*b*) as a starting point, and searched for additional literature by adding the search terms 'diet/prey' along with 'preference', 'selection' and 'profile' (together with the names of the focal species), to locate studies related to the two felids and their prey species. Finally, we compiled data on densities of wild ungulate herbivores, leopards, and tigers from systematic nationwide surveys in India (Jhala, Qureshi & Nayak, 2020; Jhala, Qureshi & Yadav, 2021) to make predictions about the strength of competition imposed by wild prey availability, across selected Protected Areas for which density estimates were available.

Literature searches (and data extraction from other sources) conducted from January to July 2022 yielded potential sources of data from 135 sources. We excluded 17 of these studies from the analyses because they did not meet our criteria: information reported was unclear/insufficient; they contained only one of the three focal species; or the paper was a review of other studies already included in our analysis. Our final list of 118 data sources (see online Supporting Information, Appendix S1) covered a timeline spanning ∼150 years (1871 to 2022) across 62 locations, from which information on direct dyadic encounters, population-level interactions, prey biomass or prey densities were extracted. Details of all the data sources are provided in Appendix S1.

III. SPECIES PROFILES

(1) Dhole

Dholes, also called Asiatic wild dogs, are social carnivores that occur predominantly in forested habitats in South and Southeast Asia (Kamler *et al.*, 2015). India has the largest population of dholes, followed by Thailand and Myanmar which still have significant populations. Bhutan, Cambodia, China, Indonesia, Laos, Malaysia and Nepal are thought to support small populations (Kamler *et al.*, 2015). Individual dholes weigh 15–20 kg. Packs of 2–25 individuals routinely hunt wild ungulate herbivores that are 5–10 times their body size (Johnsingh, 1982; Venkataraman, Arumugam & Sukumar, 1995; Srivathsa, Kumar & Karanth, 2017). Studies examining dhole distribution and habitat associations suggest that, although generally restricted to forested Protected Areas, dholes also use unprotected secondary forests, multi-use forest fragments, and agroforests adjoining Protected Areas for movement and dispersal (Jenks *et al.*, 2012; Gangadharan, Vaidyanathan & St. Clair, 2016; Punjabi *et al.*, 2017; Srivathsa *et al.*, 2019*a*, 2020*a*). They generally tend to show diurnal or crepuscular activity peaks (Karanth *et al.*, 2017). Dholes do not frequently prey on domestic livestock, nor do they attack people; their interactions with humans are generally considered to be benign. But livestock-related conflict between humans and dholes persists in Bhutan, Nepal and parts of Northeast India (Srivathsa *et al.*, 2020*b*).

(2) Leopard

Leopards are among the most versatile and adaptable large carnivores in the world. Found widely distributed across Africa, the Indian subcontinent, parts of China and the Russian Far East, and Southeast Asia (Stein *et al.*, 2020), they are solitary felids weighing around 50–70 kg. Leopards are generally nocturnal, although this can vary across locations and habitats (see Karanth *et al.*, 2017). Their reclusive behaviour means they are reported to be socially suppressed by co-predators like lions *Panthera leo*, spotted hyenas *Crocuta crocuta*, tigers and dholes (Johnsingh, 1982; Venkataraman *et al.*, 1995; Caro & Stoner, 2003). Studies examining prey preferences of leopards across their range suggest a varied diet. Their arboreal habits enable them to exploit primates and other tree-dwelling prey, perhaps enabling them to co-occur and persist alongside other large carnivores (Hayward *et al.*, 2006). In the Indian subcontinent, leopard populations can exist in completely human-dominated landscapes, where they feed on free-ranging/domestic dogs and livestock, and occasionally attack and consume humans (Athreya *et al.*, 2015, 2016).

(3) Tiger

Tigers are charismatic large carnivores, primarily found in forested habitats in South and Southeast Asia, and up to the Russian Far East. They typically have large spatial ranges, and inhabit temperate, tropical, mixed deciduous and evergreen forests (Goodrich *et al.*, 2022). Tiger populations have undergone drastic declines across their range; however, recent studies have shown a steady increase in tiger numbers following stringent protection efforts (Harihar *et al.*, 2018). Mostly solitary and nocturnal, adult tigers can weigh up to 250 kg, and can prey on herbivore ungulates that are more than four times their body mass (Karanth & Sunquist, 1995; Hayward, Jędrzejewski & Jêdrzejewska, 2012; Karanth *et al.*, 2017). Tiger densities are shaped by and scale linearly with densities of medium–large wild ungulates (Karanth *et al.*, 2004). Although most source populations occur within Protected Areas, tigers in some regions have adapted to live in close proximity to human activities (livestock grazing, agriculture, minor forest produce extraction, etc.) across shared landscapes (Rayan & Mohamad, 2009; Carter *et al.*, 2013; Warrier, Noon & Bailey, 2020). Livestock depredation and isolated attacks on humans are among the key challenges for tiger conservation, particularly along forest edges of Protected Areas (Karanth & Surendra, 2018).

IV. ANALYSES AND RESULTS

(1) Rangewide spatial overlaps

We first compiled distribution range maps for the three focal carnivores from two time points: 1900 and 2020 (Stein *et al.*, 2020; Kao *et al.*, 2020; Goodrich *et al.*, 2022). To assess the extent of spatial overlap, we calculated (*i*) the extent of area occupied by the three species individually, (*ii*) proportion of range overlap for dhole–leopard and dhole–tiger, and (*iii*) proportion of range overlap for the dhole–leopard–tiger triad. In 1900, dholes were found across an area of 32.89×10^6 km^2, leopards across 41.12×10^6 km^2 and tigers across 30.24×10^6 km^2 (Fig. 2A–C). By 2020, these range sizes had reduced to 3.84×10^6, 9.49×10^6, and 1.69×10^6 km^2, respectively (Fig. 2D–F). Dhole–leopard shared 22% of their range, dhole–tiger shared 54% and dhole–leopard–tiger together shared 18% in 1900 (Fig. 2G). These shared areas decreased to 5%, 15% and 3%, respectively, in 2020 (Fig. 2H). The studies included in our database are from 62 locations across the areas where the distributions of all three species have historically overlapped (Fig. 2I; Appendix S2).

(2) Direct interactions

We collated and characterised dyadic interactions (see Table 1 for a glossary of terms) from data sources that included natural history notes, journal articles, social media and wildlife documentary films. For each incident, we extracted information on the source, year, location, species involved, and the type of interaction (Appendix S3). We classified the interactions into three broad categories: (*i*) chasing/treeing – where an encounter involved one species chasing, including cases where the chased animal took refuge in a tree; (*ii*) kleptoparasitism – where one species steals a kill made by another species; and (*iii*) mortality – intraguild predation, i.e. one predator killing the other. These interactions did not have to be exclusively of one category type nor unidirectional. For example, a single incident could involve dholes treeing a leopard followed by the pack stealing the leopard's kill; or an encounter between a tiger and a dhole pack could have resulted in the death of the tiger as well as some members of the pack (see Appendix S3).

We assigned scores to each dyadic interaction ($N = 98$; Appendix S3) in increasing intensity of competitive 'loss' for the suppressed species. The species that was chased/treed was assigned 1, the species that lost its kill received a 2, and the species that was killed during the encounter received a score of 3 (Fig. 3). The sum of these scores for each species, scaled to the total number of incidents between the corresponding species pair, gave the total competitive strength of one species with respect to the other. In this way, we calculated the competitive strength of dholes on leopards ($N = 28$) to be 1.54, and the strength of leopards on dholes was 0.14. For the dhole–tiger pairing ($N = 70$), the competitive strength of dholes on tigers was 0.54, and the strength of tigers on dholes was 1.83. Therefore, overall, tigers were dominant over dholes, and dholes over leopards (Fig. 3).

For a subset of these incidents, where information on dhole pack sizes was documented ($N = 28$; Appendix S3), we explored if the number of individuals in the pack affected the outcome of the interaction. In this analysis, we re-assigned scores exclusively from the perspective of dholes.
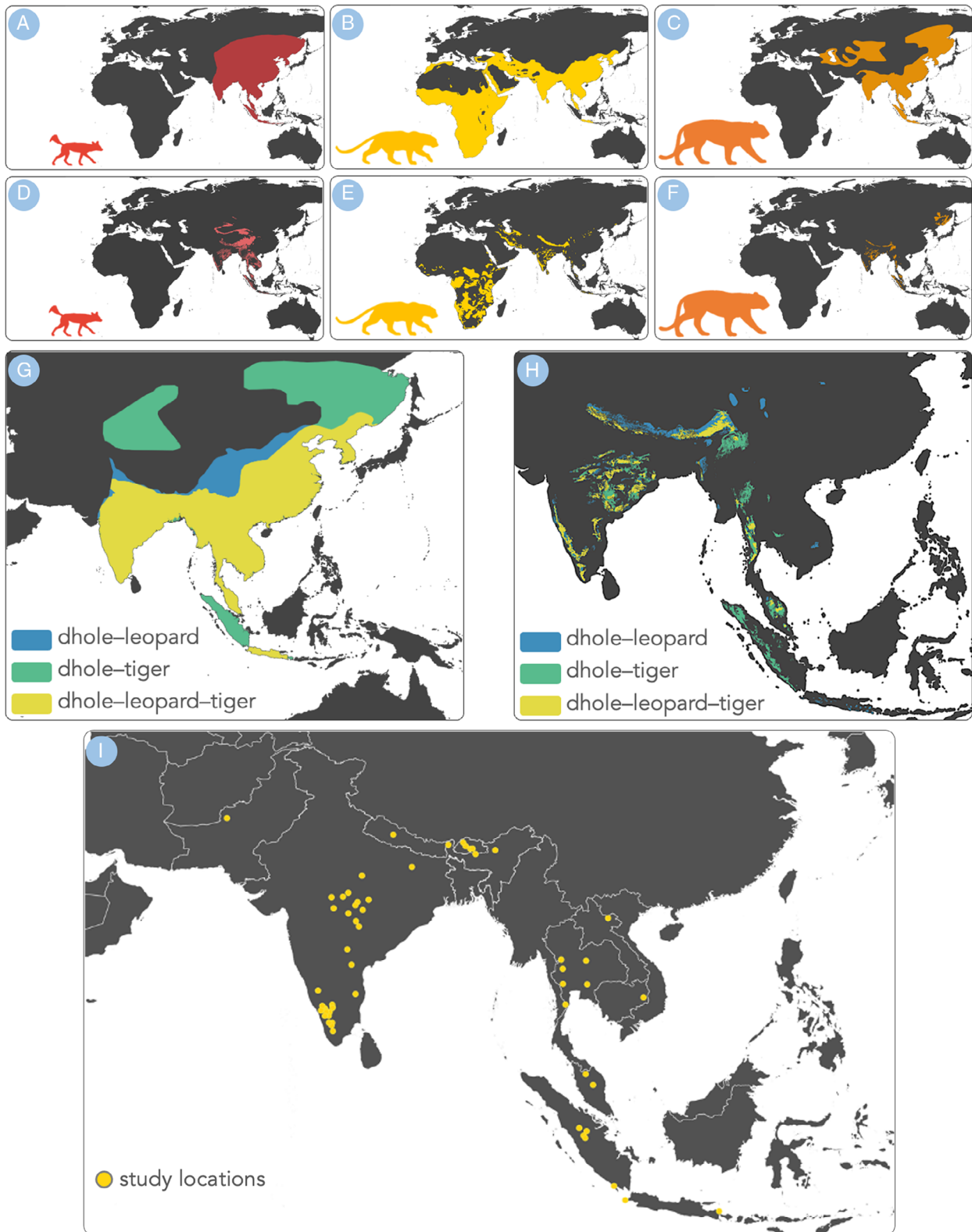
Fig. 2. (A–C) Distribution range maps for dhole (A), leopard (B) and tiger (C) in 1900. (D–F) Current distribution range maps for dhole (D), leopard (E) and tiger (F) in 2020. Data sourced from IUCN. (G, H) Range overlaps between dhole–leopard, dhole–tiger, and dhole–leopard–tiger in South and Southeast Asia in 1900 (G) and 2020 (H). (I) Locations where studies of dhole–leopard–tiger interactions used in our analyses were conducted across South and Southeast Asia. See Appendix S2 for list of study sites.

Table 1. Glossary of terms.

Dyadic interactions	Interactions between pairs (dyads) of carnivore species.
Competitive strength	Magnitude of competitive pressure (through direct interactions) of one carnivore species over the other. Dhole–leopard and dhole–tiger dyadic interactions were scored for direction and intensity of competitive strength. The competitive strength of one species with respect to the other was calculated as the sum of all scores assigned to each species in a dyadic interaction, scaled to the total number of interactions between the corresponding pair.
Prey biomass available (PBA)	Standing crop of ungulate biomass at a study site, calculated as a product of ungulate prey density (d), the body mass of prey (w = 75% of the average adult female body mass; see Jooste *et al.*, 2013) and the area of the study site (a): i.e. $d \times w \times a$. This was standardised for each study area and presented as PBA_{std}, the prey biomass per 100 km^2.
Prey biomass consumed (PBC)	Amount of ungulate prey biomass consumed by the three carnivores calculated using generalised asymptotic allometric relationships following Wachter *et al.* (2012) and Chakrabarti *et al.* (2016). Biomass consumed was calculated for each carnivore separately, scaled to a 12-month duration and summed across species to obtain PBC for each site.
Offtake threshold	Offtake threshold is the standardised prey biomass available (PBA_{std}) for the site at which the maximum proportion of available wild ungulate prey biomass is consumed by the three carnivores. This is a 'soft' threshold since the PBA does not include primate/small mammal/livestock prey.
Coexistence	Coexistence is the co-occurrence of populations of the three focal carnivore species at equilibrium, facilitated by spatial, temporal and/or dietary niche partitioning.
Prey access	Prey access is the degree to which the available prey, based on their body size, habits, and habitats, are accessible to the carnivore(s) for consumption.

In this scoring scheme, if a dhole pack stole a kill from a leopard, we assigned a score of +2 to the dhole; if a tiger killed one or more dhole individuals during an encounter, we assigned a score of −3 to the dhole; if the latter incident also involved dholes stealing the kill made by the tiger, they were scored −1 (−3 for mortality plus +2 for kill-stealing), and so on. Calculated this way, we found that leopards were consistently dominated by dholes, irrespective of the pack size (Fig. 4). Tigers, on the other hand, could generally dominate over small dhole packs but lost out during encounters with larger packs (Fig. 4).

(3) Population-level interactions

Almost all studies that examined population-level interactions among the focal species were based on camera-trap surveys ($N = 18$; 25 locations). These studies typically assessed overlap or avoidance between species pairs in space or time, or both. The extent of spatial overlap was quantified using multi-species occupancy models (Mackenzie, Bailey & Nichols, 2004), correlation coefficients (Pearson's or Spearman rank), Pianka's index (Pianka, 1973), or raw proportions of encounter locations. For temporal overlap, studies used activity kernel densities
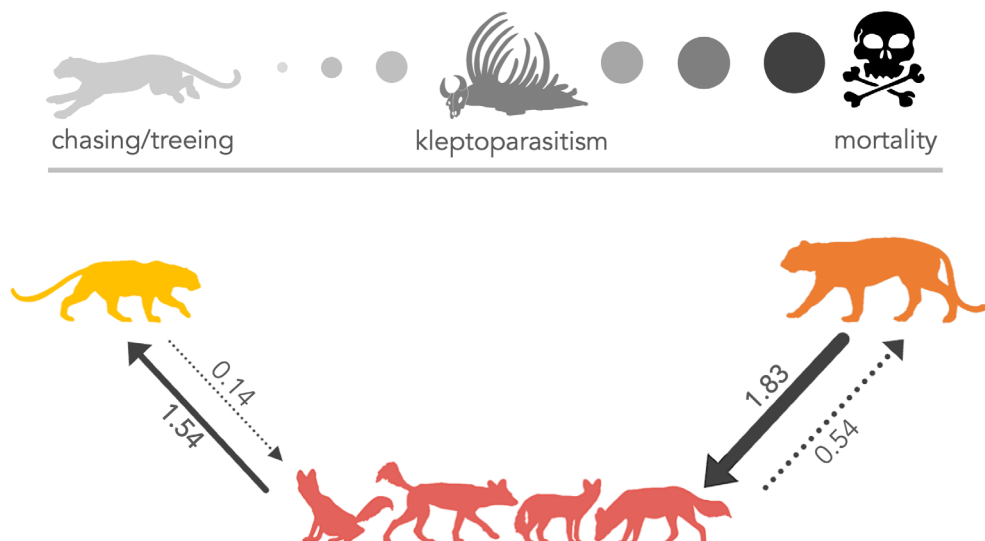
Fig. 3. Top: three categories of direct interactions analysed in this study; the species that was chased/tree'd was assigned a score of 1, the species that lost its kill (kleptoparasitism) was assigned a score of 2, and the species that was killed (mortality) was assigned a score of 3. Bottom: strength of competitive interactions between dhole–leopard ($N = 28$) and dhole–tiger ($N = 70$). Thickness of the arrows indicates magnitude of competitive strength, solid arrows denote dominance, dotted arrows denote subordinate relationship.
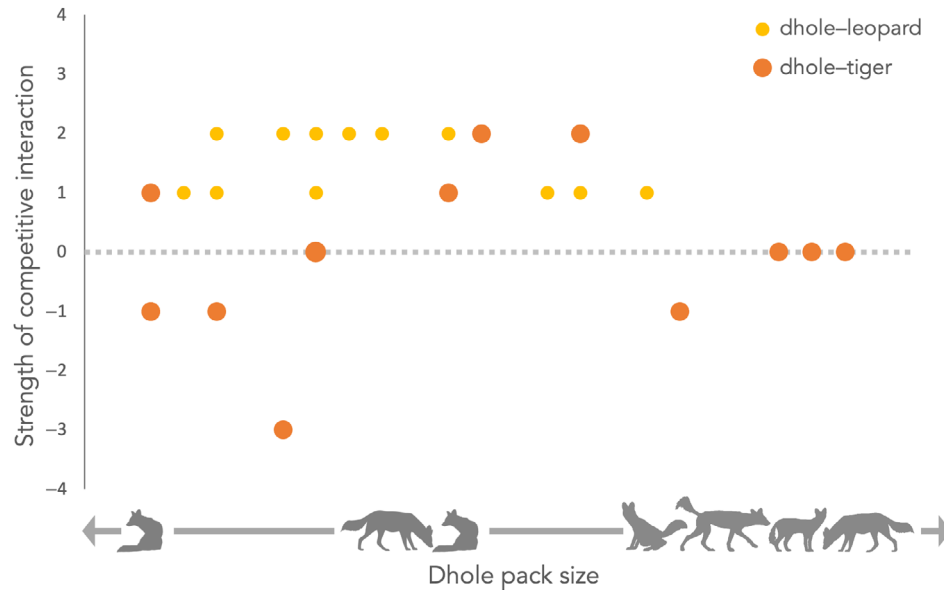
Fig. 4. Strength of competitive interactions between dholes and the two large felids (leopard and tiger), expressed as a function of dhole pack size. The *x*-axis represents dhole pack size (range = 2–23 individuals). The *y*-axis is the sum of competitive scores allocated to dyadic interactions, with each point reflecting a single dyadic interaction. In this analysis positive or negative scores were allocated to dyadic interactions exclusively from the perspective of the dholes: chasing/treeing (1); kleptoparasitism (2) and mortality (3); e.g. a dhole–tiger encounter where the tiger died is scored as +3 for dhole but if some dhole individuals were also killed this would also score −3 for dhole, giving a summed score of 0. Values above 0 reflect dholes suppressing the co-predator; values of 0 reflect overall neutral interactions; values below 0 reflect interactions where dholes are suppressed by the co-predator.

(Ridout & Linkie, 2009), correlation coefficients, Pianka's index, or raw proportions of hourly encounters. We extracted these values and rescaled them to a 0–1 range (using index-appropriate equations for numerical rescaling). We refer to these metrics as spatial interaction factor (SIF) and temporal interaction factor (TIF); values close to 0 suggest avoidance and those close to 1 suggest overlap (see Appendix S4). A few studies provided other metrics such as spatially stratified time-to-encounter between species pairs, annual population counts of the three species, etc. We collectively classified these as 'other interaction factors' (OIF; Appendix S4).

Across locations, SIF and TIF values between species pairs did not show consistent patterns of overlap or avoidance (Fig. 5). Most SIFs for dhole–leopard and dhole–tiger interactions were clustered around 0.5, indicating neither spatial overlap nor avoidance (dhole–leopard mean = 0.53; dhole–tiger mean = 0.48). TIFs for dhole–tiger interactions showed some indication of avoidance between the two species, with values tending to be <0.5 (dhole–tiger mean = 0.40; Fig. 5). Note that this analysis of SIF and TIF values reflects overall patterns and does not consider variations in predator population sizes or prey availability across locations. We did not analyse OIF data further because these values came from very few studies, and the methods used for generating them were not comparable.

(4) Diet profiles and overlap

Diet analysis was the most common approach used for understanding resource partitioning (and therefore, indirect competition) among the focal species. We compiled diet studies from 25 locations for dholes; 16 of these locations had information on leopard diet, and 14 on tiger diet (Appendices S2 and S5). For locations with multiple diet studies for any of the species, we included only the most recent assessment in our analysis. We extracted raw data on per cent occurrence of each prey species in the carnivore scats. To quantify the biomass of prey species consumed by predators, nearly all previous analyses have assumed a linear relationship between prey body mass and the biomass consumed per collectible scat of the carnivore (Floyd, Mech & Jordan, 1978; Ackerman, Lindzey & Hemker, 1984). However, recent studies have shown this relationship to be non-linear: an upper limit exists beyond which an increase in prey size does not translate to higher consumption by large carnivores (Wachter *et al.*, 2012; Chakrabarti *et al.*, 2016).

We therefore recalculated prey biomass consumed per collectible scat y using non-linear equations (Wachter *et al.*, 2012; Chakrabarti *et al.*, 2016) as:

$$y = 1.382\,(1 - \exp(0.021x))\ \text{for dhole} \tag{1}$$

$$y = 2.171 - 1.671\exp(-0.056x)\ \text{for leopard} \tag{2}$$

$$y = 2.358\,(1 - \exp(20.075x))\ \text{for tiger} \tag{3}$$

where x is the body mass of the prey species. Values of prey body mass were obtained from published information on body mass of adult females; we accounted for body size variation across prey age and size classes by taking a value of
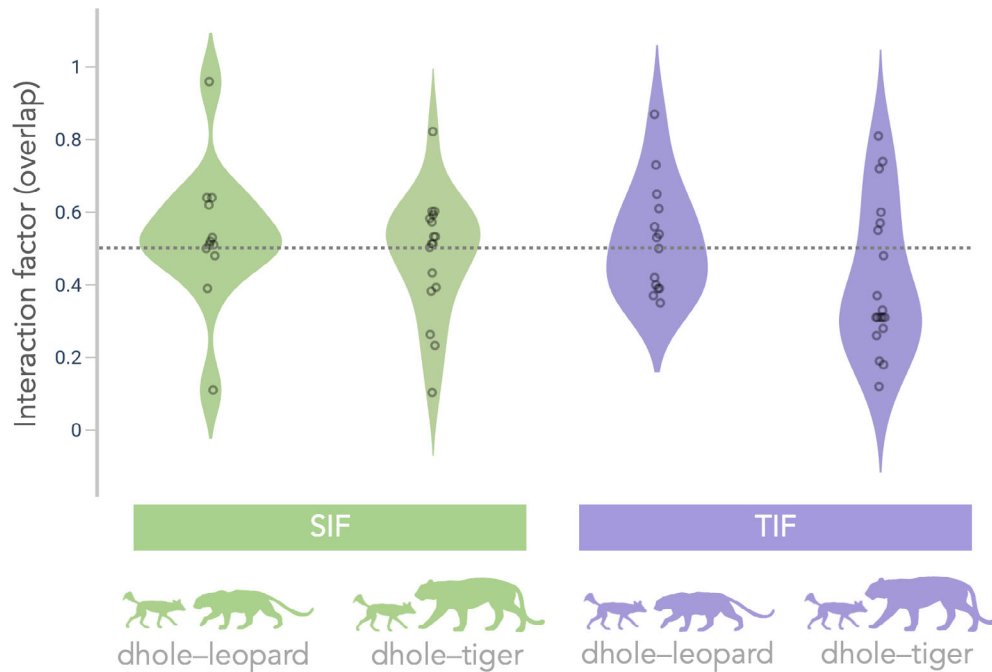
Fig. 5. Patterns of spatial interaction factor (SIF) and temporal interaction factor (TIF) across 25 locations where dhole–leopard and dhole–tiger co-occur. Values of 0.5 indicate no clear avoidance or overlap; 1 denotes full overlap and 0 denotes full avoidance between species pairs.

75% of the average adult female body mass (Jooste *et al.*, 2013). We set an upper limit of prey body mass to 200 kg because our three focal carnivores rarely consume animals above this size (Hayward *et al.*, 2006, 2012; Srivathsa *et al.*, 2020*b*). Survey durations as well as sample size (number of scats collected) varied across studies. Therefore, to allow direct comparisons, we calculated the biomass consumed (for each prey species separately) by each carnivore as % occurrence in scat multiplied by the corrected prey biomass per collectible scat, and we rescaled the values to a 12-month period (see Appendix S5).

Based on raw data, the number of prey species identified to at least genus level consumed by dhole was 49, leopard was 51, and tiger was 30 (Appendix S5). We also disregarded plant material, invertebrates, and reptiles, since these typically constitute <1% of the diet of these predators. Dhole remains were recorded in the scats of both large felids, while neither leopard nor tiger remains were recorded in dhole scats in any of the reviewed studies. Figure 6 plots the biomass consumed by each of our focal predators over a 12-month period for three prey categories: wild ungulates, primates and livestock. Tigers, on average, consumed the highest biomass of wild ungulate prey, while leopards consumed more primates and livestock as compared to dholes and tigers (Fig. 6; Appendix S5).

Steinmetz *et al.* (2021) recently carried out a region-wide synthesis of niche breadth and dietary overlap of these three carnivores using 40 studies from six countries in Asia. They found that (*i*) dhole and tiger dietary niche breadths are much narrower than that of leopards; (*ii*) niche overlap was high (>80%) for all species pairs, although marginally higher for dhole–leopard than for dhole–tiger; (*iii*) niche breadth of the carnivores correlated negatively with densities of wild ungulate prey for dhole and tiger, but not for leopard; and (*iv*) all three carnivores switched to consuming more small prey (<30 kg) at lower wild ungulate densities.

(5) Prey offtake and threshold

Based on field observations and quantitative assessments, Karanth *et al.* (2004) suggested that tigers harvest ∼10% of the available wild ungulate prey in sites where predator densities are very high. They also speculated that leopards and dholes together may take ∼5% of the available wild ungulate prey. We tested this claim using data on wild ungulate prey availability and predator diets across locations. We also calculated % offtake of ungulate prey, i.e. the ratio of wild ungulate prey biomass consumed to biomass available. We determined the 'offtake threshold' to be the offtake at the location with the highest prey offtake by the three carnivores combined (see Table 1). This threshold indicates the amount of prey biomass required to sustain co-occurrence of all three carnivore species at high densities.

We found studies from 15 locations where both carnivore diet analyses and prey density estimates were available. Since the required information was derived from multiple sources for some of the locations, we attempted to ensure that the diet data and prey density estimates were from similar timepoints. For all these locations (Table 2), we calculated the prey biomass available (PBA), prey biomass consumed (PBC) by the
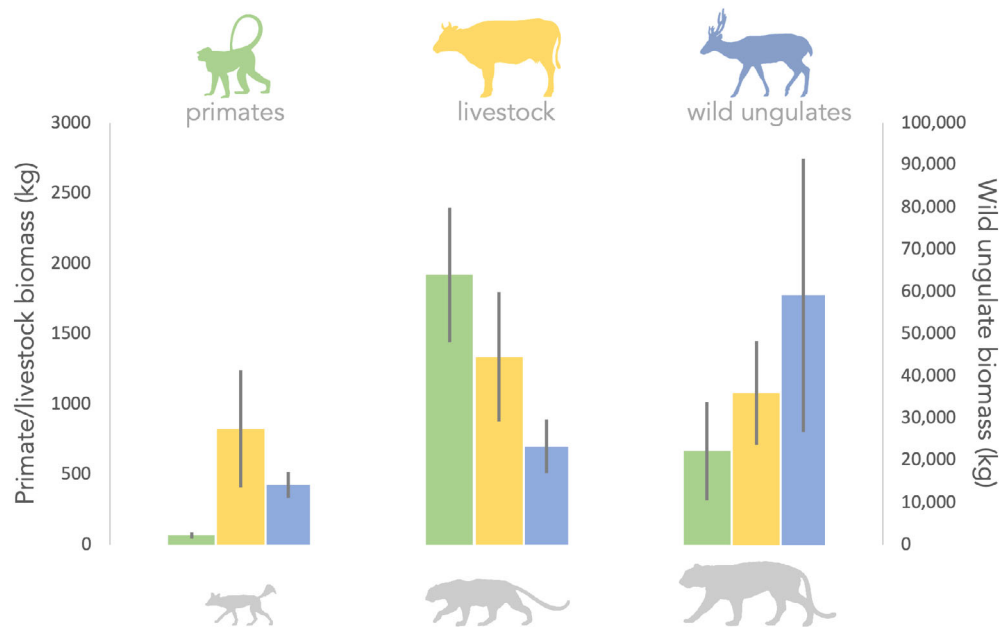
Fig. 6. Average prey biomass consumed over a 12-month period by dhole ($N = 25$ locations; left), leopard ($N = 16$; centre) and tiger ($N = 14$; right) from three prey categories: primates, wild ungulates, and domestic livestock. Vertical lines denote standard errors.

three carnivores (from equations provided in Section IV.4; see Appendices S5 and S6), and the percentage offtake (PBC/PBA × 100). The average prey offtake was 1.4% for dholes (range = 0.1–6.8), 2.6% for leopards (range = 0.2–10.2), and 4.6% for tigers (range = 0.1–22.8). Percentage offtake by the three predators is presented in Fig. S1 for each of the 15 sites. Average total offtake by all three carnivores across locations was 8.2% (range = 0.4–30.2%). The highest prey offtake was in Bandipur, India (30.2%) – where the three carnivores are at very high densities. After standardising for study area size, this

Table 2. Summary of estimates of prey biomass consumed, biomass available and per cent offtake by dholes, leopards and tigers across 15 locations based on analysis of information extracted from diet studies included in Appendix S5. Total biomass includes all prey items; PBA_{std} is the prey biomass available per 100 km^2. The row in bold denotes the maximum calculated % offtake by the three carnivores; the corresponding value of PBA_{std} is the offtake threshold.

Site	Total biomass consumed (kg ×10^{-3})	Wild ungulate prey biomass consumed (PBC; kg ×10^{-3})	Wild ungulate prey biomass available (PBA; kg ×10^{-3})	% Offtake (= 100 × PBC/PBA) by dhole, leopard and tiger	Study area (km^2)	PBA_{std} [(kg/100 km^2) × 10^{-3}]
PR	112.46	104.01	1687.25	6.16	275	613.54
AM	170.19	145.31	5630.95	2.58	958	587.78
EK	8.53	7.79	402.79	1.93	97	415.25
MM	182.14	173.28	679.56	25.5	187	363.4
NH	68.48	65.28	350.79	18.61	104	337.3
PN	52.56	49.27	1269.71	3.88	410	309.69
BP	**646.81**	**620.86**	**2053.92**	**30.23**	**880**	**233.4**
SP	101.65	90.98	445.56	20.42	336.7	132.33
PK	84.6	76.5	1089.64	7.02	862	126.41
KM	21.74	15.87	1003.64	1.58	900	111.52
TL4	11.56	10.65	1573.48	0.68	2780	56.6
BT1	20.74	11.99	760.43	1.58	1723	44.13
CM$^\$$	21.7	19.24	1248.21	1.54	3725	33.51
LS*	4.03	3.22	1562.17	0.41	3000	26.26
TL5	1.29	0.58	95.79	0.6	969	9.89

Values of total biomass consumed, PBC, PBA and PBA_{std} are rescaled (×10^{-3}) for ease of representation. Sites PR to KM are in India: PR, Parambikulam; AM, Anamalai; EK, Eravikulam; MM, Mudumalai; NH, Nagarahole; PN, Pench; BP, Bandipur; SP, Satpura; PK, Pakke; KM, Kalakad. TL4, Huai Kha Kaeng, Thailand; BT1, Jigme Singye, Bhutan; CM, Srepok, Cambodia; LS, Nam Et-Phou Louey, Laos; TL5, Kuiburi, Thailand.
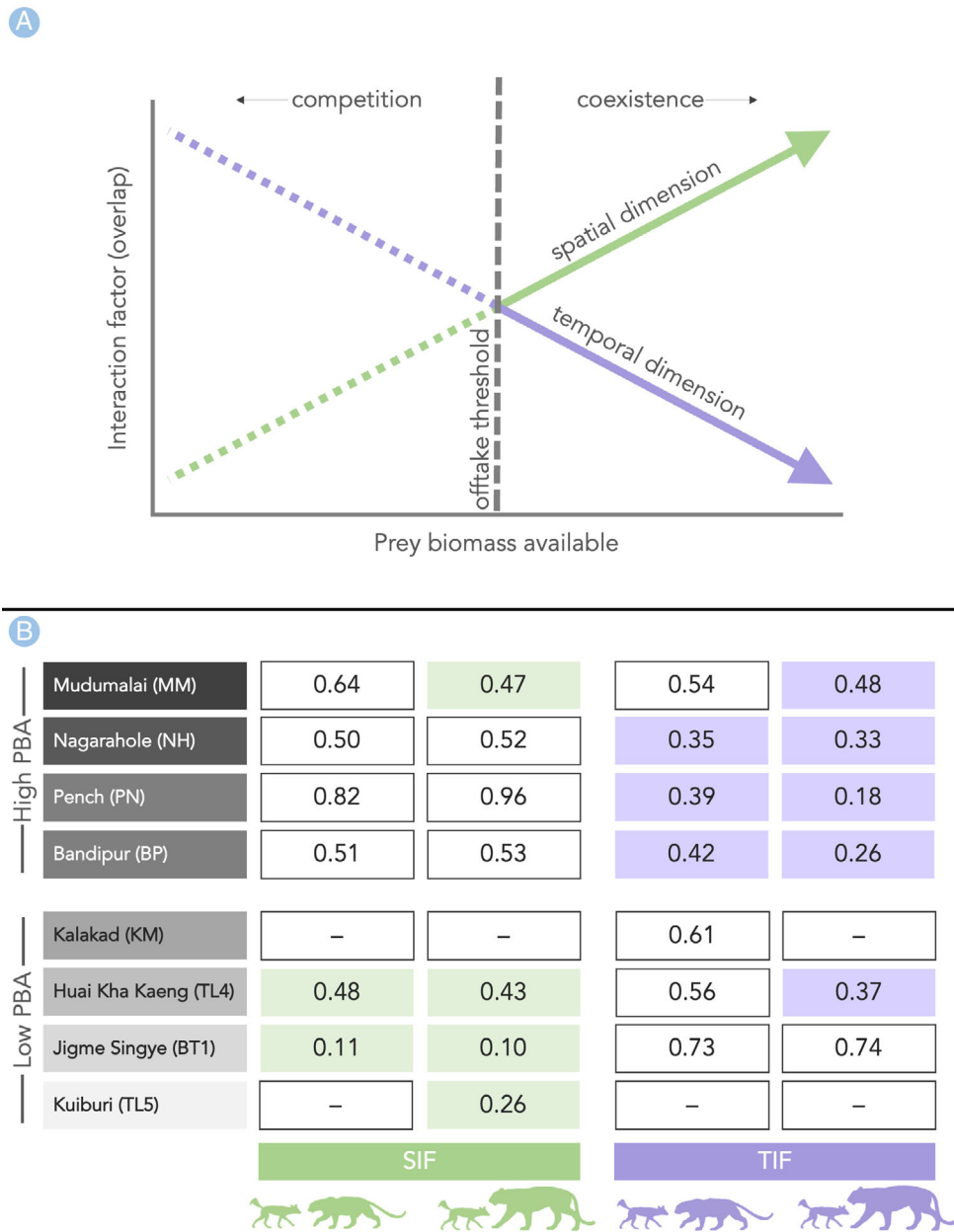$^\$$Tiger was locally extinct in Srepok, Cambodia, during the study period.
*Leopard was locally extinct in Nam Et-Phou Louey, Laos, during the study period.

represented an 'offtake threshold' of 233,400 kg/100 km² of available prey biomass (Table 2).

(6) Linking prey availability and competitive interactions

Availability of and access to primary resources theoretically mediates competition between species. In the three niche dimensions that govern competition between large carnivores, prey availability is thought to be the primary resource (Clements *et al.*, 2014; Greenville *et al.*, 2014; Périquet *et al.*, 2015). To investigate whether this is the case for our triad of predators, we examined competition-driven resource partitioning in space and time (overlap or avoidance, i.e. SIF and TIF) across a gradient of prey availability. We predicted that when prey availability is low, carnivores would avoid each other in space to reduce interference competition; to compensate for being spatially constrained while

		SIF	SIF	TIF	TIF
High PBA	Mudumalai (MM)	0.64	0.47	0.54	0.48
	Nagarahole (NH)	0.50	0.52	0.35	0.33
	Pench (PN)	0.82	0.96	0.39	0.18
	Bandipur (BP)	0.51	0.53	0.42	0.26
Low PBA	Kalakad (KM)	–	–	0.61	–
	Huai Kha Kaeng (TL4)	0.48	0.43	0.56	0.37
	Jigme Singye (BT1)	0.11	0.10	0.73	0.74
	Kuiburi (TL5)	–	0.26	–	–

Fig. 7. (A) Schematic diagram depicting our hypothesis on how prey biomass availability will affect population-level spatio-temporal interactions among carnivore pairs. Below the offtake threshold, we expect higher intraguild competition, reflected in low spatial interaction factor (SIF) and high temporal interaction factor (TIF) values. Above the offtake threshold, intraguild competition is relaxed, with high SIF and low TIF values predicted. (B) Eight locations with information on prey biomass available (PBA) and at least one metric of SIF or TIF available for dhole–leopard or dhole–tiger interactions. Filled boxes indicate values <0.5, i.e. avoidance between species pairs.

still meeting their prey requirements, they would remain active for more hours and thereby show higher temporal overlap. However, when prey availability is high, carnivores would not avoid each other in space because this resource no longer represents a constraint. This would translate to narrow peak(s) in temporal activity because they would not need to devote long periods towards meeting their resource requirements. Taken together, low-prey-density areas should show signatures of higher competition (low SIF, high TIF), and high-prey-density areas should enable co-predator coexistence (high SIF, low TIF; Fig. 7A).

We set 'low' and 'high' prey availability to be prey availability lower or higher respectively than the prey availability at the offtake threshold (see Section IV.5). Among the reviewed studies, eight locations had data on prey availability, together with at least one metric of population-level interaction (SIF and/or TIF for dhole–leopard and/or dhole–tiger). Four of these locations were low-PBA locations, i.e. prey availability was lower than that at the offtake threshold, and four were high-PBA locations (Fig. 7B). The observed patterns of SIF and TIF generally agreed with our predictions. At low-PBA locations, studies reported spatial avoidance and temporal overlaps between both species pairs, and at high-PBA locations, studies reported spatial overlap (or non-avoidance) but temporal segregation (Fig. 7B). In the latter case, we note that segregation in the temporal niche may not be 'avoidance' *per se*; rather, it could be the non-overlapping of temporal activity because the carnivores do not *need* to be active during each other's period(s) of high activity/movement. We do note that these inferences are somewhat limited by a small size of eight locations, and suggest that future studies make simultaneous assessments of prey availability/offtake linked to predator spatio-temporal interactions.

V. CONSEQUENCES OF RESOURCE-MEDIATED COMPETITIVE INTERACTIONS

Having established links between carnivore spatio-temporal partitioning and prey availability *via* the offtake threshold, we were interested in using these results to make predictions about carnivore competition and coexistence in other locations. To generate realistic predictions we incorporated information on predator densities from nationwide surveys in India, which provide temporally synchronous estimates of tiger, leopard and prey densities (Jhala *et al.*, 2020, 2021). We compiled estimates from 40 Protected Areas (PAs) for which (*i*) densities of tigers, leopards and prey species were all available, and (*ii*) they were located within the shared distributions of dhole, leopard and tiger (Fig. 8; Appendix S7). Estimates of dhole densities were available only for two of these PAs so we did not include dhole in this assessment. We converted prey density estimates into biomass for consistency with our other analyses, and found a linear correlation of combined predator (leopard and tiger) densities with PBA (Fig. 8; *sensu* Karanth *et al.*, 2004).

Of the included PAs, 20 had a prey biomass that was lower than our 'offtake threshold' and 20 were above this threshold (Fig. 8). We consider the value of 233,400 kg/100 km^2 a 'soft' threshold because our metric of PBA was made for only wild ungulate prey, hence excluding primates, small prey and livestock. For the 20 PAs with a PBA lower than our offtake threshold biomass, we predict that the strength of intraguild interactions will be inversely correlated with PBA (Fig. 9). So, in PAs such as Udanti, Palamau, Anamalai and Buxa, intraguild competition is likely to be very high; this could be empirically tested with surveys of population-level interactions. If our prediction holds true, these PAs would have very low SIFs and high TIFs between species pairs, and perhaps

$$y = 4.46 + 2e\text{-}05x$$
$$R^2 = 0.35 \, ; \, p < 0.001$$
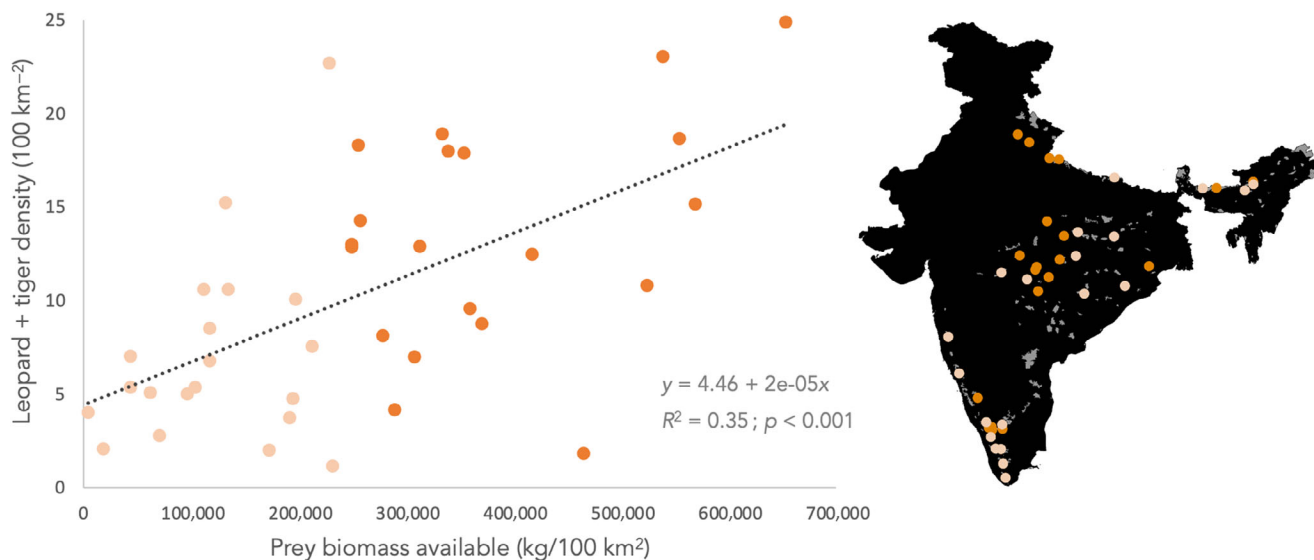
Fig. 8. Relationship between prey biomass available (PBA) and carnivore densities (leopard + tiger) across 40 Protected Areas (PAs) in India. Light circles are PAs with PBA < offtake threshold, dark circles are PAs with PBA > offtake threshold. The map on the right shows the locations of the 40 PAs in India. Grey patches are other PAs within the dhole–leopard–tiger range overlap region.

competitive exclusion of one or more carnivore species in extreme cases.

With increasing PBA, predator densities increase linearly (Fig. 8). When predator densities increase, their home-range sizes contract (Efford *et al.*, 2016), and intraguild competition is replaced by density-dependent conspecific competition. In forested PAs of South and Southeast Asia, space is a limiting resource. Here, high predator densities and consequent conspecific competition may force individuals towards forest-edge habitats; this could translate to greater contact with and depredation of domestic livestock (see Srivathsa *et al.*, 2020*b*). In the 15 locations for which we assessed prey offtake (Table 2, Appendix S6; note that in Table 2, Nepal 'NP' was excluded from the 16 locations listed in Appendix S6 because PBA data were not available), the average livestock biomass consumed by the three predators in high-PBA locations was more than twice that in low-PBA locations (4149 *versus* 1948 kg; Appendix S6). We therefore predict that in the 20 PAs where PBA is higher than our threshold, the probability of livestock depredation (along PA edges) will be positively correlated with leopard and tiger densities (Fig. 10). Based on this prediction, areas surrounding PAs like Rajaji, Corbett, Panna and Pench would have the highest levels of livestock depredation.

VI. DISCUSSION

Interspecific competition remains a focus of ecological investigations, with studies continuing to generate new patterns and mechanisms that ultimately define species assemblages, distributions, adaptations and persistence (Macarthur & Levins, 1967; Connor & Simberloff, 1979; Caro & Stoner, 2003; Prugh *et al.*, 2009). Our study adds to this growing body of work, filling a prominent gap regarding rangewide interactions among apex carnivores in Asia's forest systems. To the best of our knowledge, this is the first assessment that quantifies the ecological thresholds in the dietary dimension that determine interactions in spatial and temporal dimensions, thereby linking the three niche dimensions that fundamentally govern carnivore competition.

(1) Novel data sources enable macro-ecological assessments

Addressing questions at the global or continental levels can reveal interesting broad-scale insights on species ecology. Such assessments require large data sets or carefully tailored syntheses based on extensive literature (Chapron *et al.*, 2014;
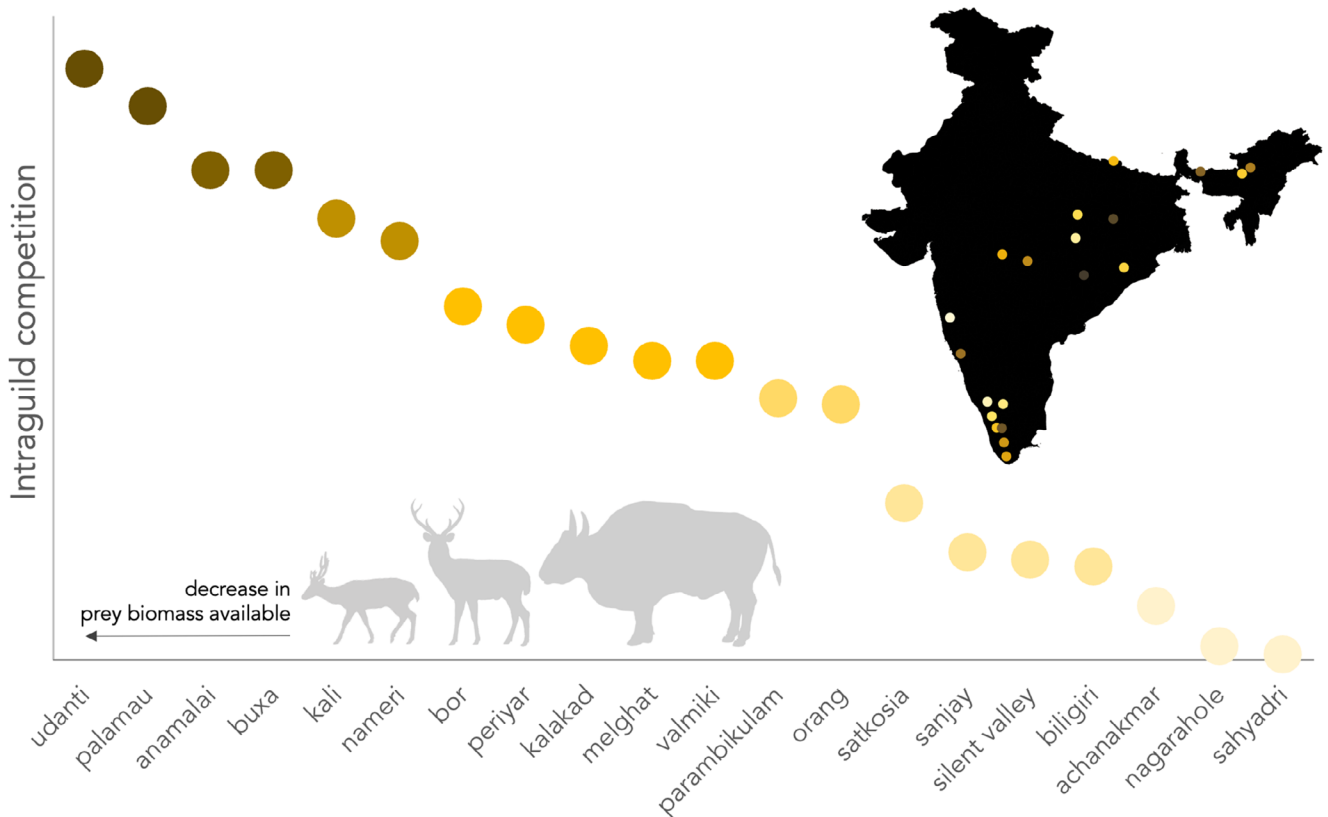
Fig. 9. Predicted intraguild competition for 20 Protected Areas (PAs) in India where prey biomass available (PBA) is lower than our offtake threshold of 233,400 kg/100 km² (see Section IV.5 and Table 2). The PAs are arranged in decreasing order of PBA, which is assumed to correlate inversely with levels of intraguild competition among the carnivores. Based on this assumption, PAs on the left will have the highest levels of intraguild competition, leading to competitive exclusion of one or more carnivore species. Note that some of these PAs are within the putative range of all three carnivores, but one or more species may already be locally extinct.
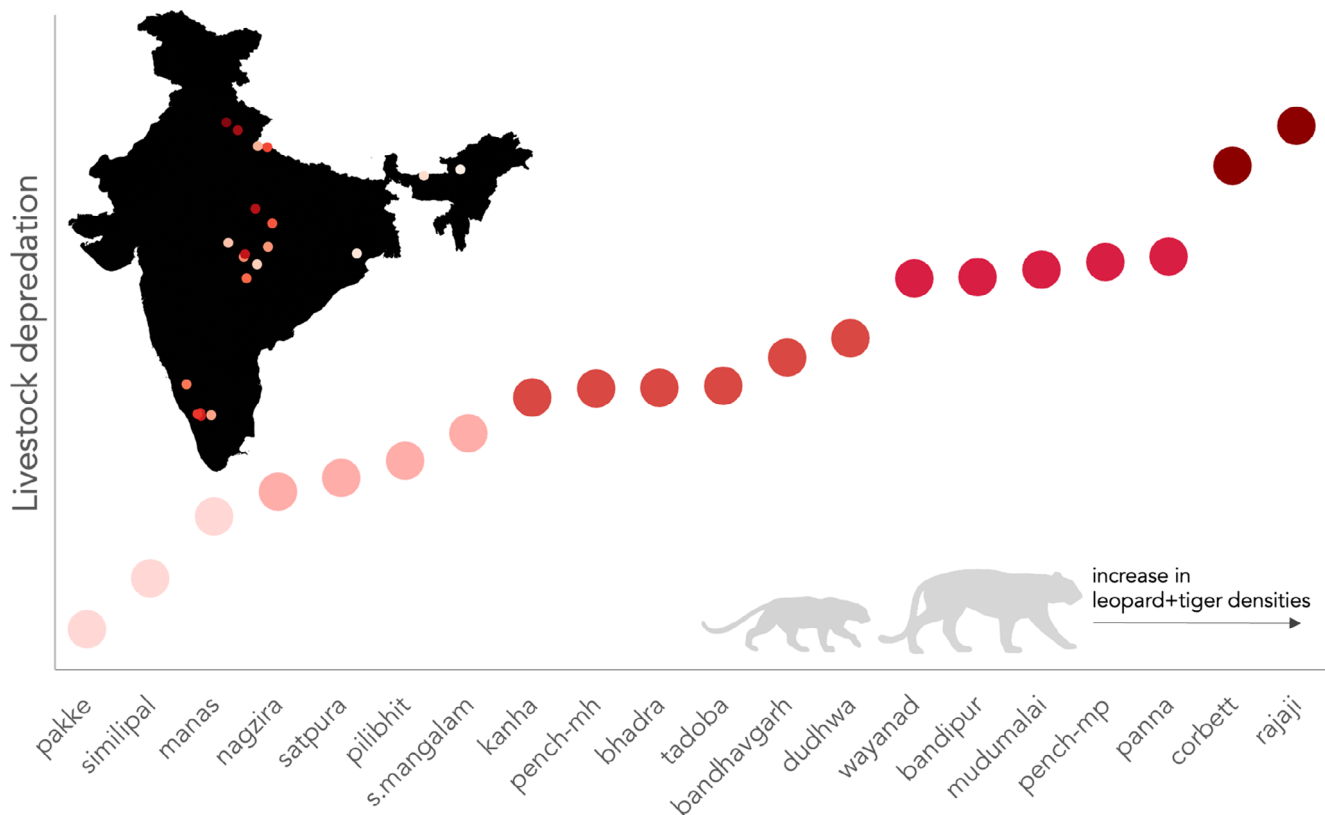
Fig. 10. Predicted likelihood of livestock depredation for 20 Protected Areas (PAs) in India where prey biomass available (PBA) is higher than our offtake threshold of 233,400 kg/100 km² (see Section IV.5 and Table 2). The PAs are arranged in increasing order of carnivore (leopard + tiger) densities, which is assumed to correlate directly with predicted levels of livestock depredation by these carnivores. Based on this prediction, PAs on the far right will have the highest levels of livestock depredation by these carnivores. Note that some of these PAs are within the putative range of all three carnivores, but one or more species may already be locally extinct.

Sévêque *et al.*, 2020). Conducting such syntheses, systematic reviews or meta-analyses for regions and countries that are data-poor, or do not have a long history of conducting quantitative research, can impose challenges and limitations (Srivathsa *et al.*, 2022). With the advent of smart technology and the widening of access to web-enabled devices, the internet can serve as a powerful tool for overcoming some of these challenges. For example, social media platforms like Twitter and Instagram are enabling the acquisition and analyses of novel data for researchers investigating various aspects of ecology, wildlife trade, nature-based tourism, and allied themes (Tenkanen *et al.*, 2017; Di Minin *et al.*, 2018; Jarić *et al.*, 2020; Edwards, Jones & Corcoran, 2022). In a recent study, Curveira-Santos *et al.* (2022) showed how data sourced from *Google Images* could improve (and challenge) current understanding of intraguild interactions among African carnivores. With limited published information available on direct interactions among dholes, leopards and tigers, our study demonstrates the utility of unconventional data sources (social media and wildlife documentaries) for examining macro-ecological patterns, especially in data-constrained regions.

(2) Sociality can alter dominance hierarchy

Interference competition, and therefore dominance, plays an important role in maintaining carnivore community structures, with consequences for population demography and dynamics (Linnell & Strand, 2000). Most of our knowledge on interference competition among large predators comes from the African savannas, where lions, spotted hyaenas, leopards, painted dogs *Lycaon pictus*, and cheetahs *Acinonyx jubatus* co-occur at relatively high densities (Swanson *et al.*, 2014, 2016). Except for the leopard, all other species show some degree of sociality, which either alters or adds to the complexity of intraguild interactions (Creel & Creel, 1996; Périquet *et al.*, 2015). For our focal species, dholes are social while both felids are solitary. Albeit simplistic, our scoring scheme for interference competition showed that tigers exert more competitive pressure on dholes, than do dholes on leopards. This was also somewhat reflected in the SIF scores; in low-prey-density areas where all three predators co-occur, the average SIF for dhole–leopard was 0.40 and that of dhole–tiger was 0.36, indicating marginally higher avoidance in the latter pair (see Appendix S4).

Sociality offers dholes a clear advantage over leopards, and to a limited extent, over tigers (Fig. 4). Based on a modest set of observations from southern India, Karanth & Sunquist (2000) surmised that dholes and tigers are both dominant over leopards. Our results offer greater clarity on this dominance hierarchy (tiger > dhole > leopard) based on more data records from a much wider geographic area. We acknowledge the possibility of inaccuracies in historical records of game hunters and naturalists. But the overall inferences we draw nonetheless quell several unsubstantiated notions on this topic, particularly about dhole–tiger relationships (Burton, 2019).

(3) Habitat structure and prey mediate spatio-temporal interactions

Protected Areas of Asia where most source populations of dholes, leopards and tigers are found are on average ∼650 km^2 in size – much smaller than Protected Areas in Africa, Europe or North America. Forests are primary habitats for all three species; these forest habitats are heavily fragmented and degraded across the continent (Joshi *et al.*, 2016; Nayak *et al.*, 2020). Further, human populations reach much higher densities in South and Southeast Asia (160–350/km^2) as compared to Africa (45/km^2), Europe (34/km^2) or North America (20/km^2; www.worldpop.org). Human presence and associated activities can act as social barriers to carnivore presence and movement, particularly within shared forest habitats outside designated Protected Areas (Puri *et al.*, 2022). Space is thus inherently a limiting resource for these three carnivores, although vertical habitat structure can facilitate fine-scale spatial avoidance. Leopards, for instance, exploit arboreal habitats to escape risky encounters and also to cache their kills (Karanth & Sunquist, 2000). Dholes use dens during the breeding season; these are typically underground or in cavities in rocky habitats that are too small for the two large cats to enter (Johnsingh, 1982). Such avoidance mechanisms are important for enabling co-predator coexistence, but unlikely to be captured by studies using spatially static camera-trap data.

The role of prey as a mediating factor in carnivore intraguild competition is well established (e.g. Kortello, Hurd & Murray, 2007; Greenville *et al.*, 2014). Studies from open-habitat systems have shown how dead prey, i.e. carrion, can also be crucial in shaping carnivore co-occurrence, through kleptoparasitism and scavenging opportunities (Creel, 2001; Périquet *et al.*, 2015). Unfortunately, dense tropical and sub-tropical forests make detailed observations on kill-stealing or scavenging events difficult, and the data presented herein may be inadequate in this respect. We do show however that at the population level, wild prey availability is a pivotal factor that may dictate the rules of competition among the three focal carnivores. We used data from Bandipur (India) to calculate the prey 'offtake threshold', where all three carnivores reach very high densities [leopards + tigers 18/100 km^2 (Jhala *et al.*, 2020, 2021); dholes 12–14/100 km^2 (Srivathsa *et al.*, 2021)]. Our results confirm

and add to the patterns reported by Karanth *et al.* (2017) with respect to prey-mediated temporal activity of the three species. Carnivore pairs in low-prey locations showed spatial segregation; but they were active for longer periods (presumably to maximise prey acquisition), and thereby showed higher levels of temporal overlap (Fig. 7). Since heightened temporal activity incurs higher bioenergetic costs, a pertinent topic of future research would be to evaluate its impacts on demographic attributes like survival and reproductive success.

(4) The competition–coexistence spectrum in tropical systems

In Section IV.6 we suggested that prey offtake mediates carnivore spatio-temporal interactions, essentially proposing a continuum of competition to coexistence, mediated by prey availability. At one extreme of this spectrum, competitive exclusion likely results in the eventual elimination of a subordinate predator (Linnell & Strand, 2000). In Kuiburi (Thailand), a location with among the lowest PBA (TL5 in Table 2), Steinmetz *et al.* (2013) reported complete spatial segregation between dholes and tigers. We predict that, if depressed prey numbers remain unchanged, Protected Areas such as Udanti, Palamau and Buxa in India may exhibit similar trajectories. In parts of Southeast Asia where prey densities are very low, this pattern is further altered through the direct persecution of predators by humans. Leopards and tigers are now extinct in Nam Et-Phou Louey, Laos (Rasphone *et al.*, 2019), and tigers have been eliminated from Srepok, Cambodia (Harihar *et al.*, 2018). In such cases, the extremely high degree of human impacts completely eclipses the ecological and behavioural determinants of intraguild interactions.

On the other side of the spectrum, we expect that an increase in prey biomass availability will foster co-predator coexistence. We note, however, that the mechanisms that allow for such coexistence may be complicated by prey *access* (Table 1). Using our offtake threshold of 233,400/100 km^2, this translates to ∼1000 individuals of large prey (gaur *Bos gaurus*, sambar *Rusa unicolor*, banteng *Bos banteng*), which are more accessible to tigers or very large dhole packs, or to 5000–8000 medium-sized prey (e.g. spotted deer *Axis axis*, wild pigs *Sus scrofa*), typically targeted by leopards and medium-sized dhole packs, or to ∼15,000 small ungulate prey (e.g. muntjac *Muntiacus muntjak*, four-horned antelope *Tetracerus quadricornis*), which are suitable prey for very small dhole packs or lone dhole individuals. Assessing and incorporating this aspect of prey *access* is extremely difficult in tropical forest settings, where we typically do not have information on prey age/size classes. We therefore followed standard approaches of measuring biomass available and biomass consumed, which is a conservative yet reliable way to assess predator–prey relationships (see Steinmetz *et al.*, 2021).

At the extreme end of this spectrum, we predict that very high wild prey availability and the ensuing increase in predator densities will lead to higher chances of livestock

depredation at the forest fringes (see Suryawanshi *et al.*, 2017; Srivathsa *et al.*, 2020b). Here again, fine-scale factors affecting access to livestock, and the different propensities of the three carnivores to pursue domestic prey (Ramesh *et al.*, 2020) will determine the actual levels of livestock depredation. This warrants an empirical evaluation of livestock depredation levels using a uniform methodology across locations. However, our predictions match with losses attributed to leopards and tigers in five Protected Areas of India (Sathyamangalam, Kanha, Bhadra, Tadoba and Bandipur) where comparable survey designs were employed (Karanth & Ranganathan, 2018; Karanth & Surendra, 2018).

(5) Data limitations and analytical considerations

Considering the large timeframe and the range of data sources used here, our synthesis has certain limitations. (*i*) We examined interactions among three carnivores, with dhole as the primary focus. The two large felids also have interesting dynamics with each other, including direct interference competition, spatio-temporal partitioning (Karanth *et al.*, 2017), diet overlap (Lovari *et al.*, 2015), physiological responses (Patel *et al.*, 2023) and demographic impacts (Harihar, Pandav & Goyal, 2011), that were not considered in our assessment. Since both felids are nocturnal, spatio-temporal segregation typically manifests as fine-scale avoidance (see Lahkar *et al.*, 2021; Chatterjee *et al.*, 2023; see Figs S2 and S3). (*ii*) Our literature searches revealed records of interactions between dholes and other carnivores like snow leopard *Panthera uncia* (Gruisen, 1993), clouded leopard *Neofelis nebulosa* (Rasphone, Kamler & Macdonald, 2020), Asiatic golden cat *Catopuma temminckii* (Kawanishi & Sunquist, 2008), etc.; these species pairs were not included in our analysis. (*iii*) Direct interactions between species pairs are unlikely to be documented if they were uneventful, i.e. when encounters did not involve chasing, kleptoparasitism, or mortality, creating an observation bias wherein non-agonistic encounters are under-represented in the literature. (*iv*) The SIF and TIF values used here were derived from different types of analyses, ranging from statistically robust model-based estimates (multi-species occupancy) to raw proportions (which do not incorporate detection biases). (*v*) Population-level interactions measured as 'time-to-encounter' metrics provide a better understanding of fine-scale avoidance between species pairs (Lahkar *et al.*, 2021). We could not formally synthesise such results because only three studies used this type of analysis. (*vi*) All diet assessments considered here relied on visual examination of scats to determine the identity of the carnivore. Since these were not verified, e.g. by using genetic methods, we cannot discount the possibility of species misidentification (Morin *et al.*, 2016).

VII. CONCLUSIONS

(1) Dholes, leopards and tigers have experienced massive range contractions during the last century, and are now locally extinct across 95%, 82% and 79% respectively of their former ranges (Wolf & Ripple, 2017). Areas where they currently co-occur represent only <3% (364,600 km²) of their collective distribution extents. Their source populations are mostly found within Protected Areas (31% of shared areas), which are typically resource-rich 'islands' with hard habitat edges. All three species occur outside Protected Areas (Puri *et al.*, 2019, 2022; Srivathsa *et al.*, 2020a), but their resilience in such sub-optimal habitats varies: highly adaptable leopards thrive relatively well, while tigers can disperse long distances through human-use landscapes, but dholes are more forest-restricted (Joshi *et al.*, 2013; Athreya *et al.*, 2015; Srivathsa *et al.*, 2019b). We suggest that the consequences of intraguild competition would be interesting to explore outside designated Protected Areas, specifically to evaluate their potential to support co-occurrence of the three carnivores in the long term.

(2) The three species we focus on also co-occur (albeit marginally) with other medium and large carnivores like grey wolf *Canis lupus*, golden jackal *Canis aureus*, snow leopard, clouded leopard, black bear *Ursus thibetanus* and brown bear *Ursus arctos* (Wolf & Ripple, 2017; Srivathsa *et al.*, 2020b). The interplay amongst predators in multi-carnivore systems is likely to be more complex, with consequences for prey offtake, spatio-temporal activity patterns, and potentially, sociality and population sizes. A detailed assessment in one or more such locations, examining interactions linking all the species and transcending trophic levels, would broaden current understanding of intraguild competition in tropical forest systems.

(3) Our results from quantifying direct interactions among the three predators hint at how dominance hierarchies may be altered when sociality (group-living) offers a competitive advantage to one species over the other(s). A meta-analysis by Bhandari *et al.* (2021) indicated that dhole pack sizes (across locations) may be shaped by tiger densities. Data on dhole pack sizes, seasonal/annual dynamics and intra-pack interactions remain poorly understood. Future studies focused on dhole–leopard–tiger sympatry could allow us to fill this knowledge gap on dhole sociality.

(4) Population-level interactions involving spatial and temporal overlap or avoidance among the focal species have been examined almost exclusively using camera traps. We use the same data to make inferences on the breadth of temporal niches for these carnivores across a gradient of prey availability. In both cases, we draw process-related inferences from observed patterns. Data from telemetry studies on multiple individuals could provide more reliable information on both these aspects (see Vanak *et al.*, 2013). Such studies could also offer better insights on interference competition, facilitation (kleptoparasitism or scavenging) and intraguild predation.

(5) Human presence and associated activities such as forest-grazing livestock may cause carnivores to alter their spatio-temporal activities (Carter *et al.*, 2015; Sévêque *et al.*, 2020). Targeted poaching or harvest of one or more predators may also change competition dynamics among species (e.g. Nam Et-Phou Louey, Laos and Srepok, Cambodia).

The locations from which we analyse patterns of sympatric interactions vary widely in terms of their protection histories and intensities, management regimes and anthropogenic pressures. While their impacts may be reflected somewhat indirectly in the underlying population sizes of these carnivores and their prey (Karanth *et al.*, 2004), studies tailored explicitly to investigate these factors would allow for directly gauging their impacts on intraguild interactions.

(6) Dietary niche partitioning entails predators selecting different prey species, or individuals of different age/size classes (Elmhagen *et al.*, 2010). For our focal species, several meta-analyses have examined rangewide patterns in niche partitioning (Hayward *et al.*, 2006, 2012; Srivathsa *et al.*, 2020*b*; Steinmetz *et al.*, 2021). Almost all studies they included were based on examination of faecal remains, which (*i*) may not provide a comprehensive list of all prey items consumed, and (*ii*) do not allow inferences on preferences for specific prey age/stage classes. Combining recent developments in molecular methods (like DNA meta-barcoding; Shi *et al.*, 2021) and information from direct observations of kills to classify prey age or size class (e.g. Karanth & Sunquist 2000; Ghaskadbi, Nigam & Habib, 2022) could address both these issues and help elucidate nuances in dietary niches and segregation.

(7) Translocation or reintroduction of large carnivores is now an established management practice across landscapes, countries and regions (Fontúrbel & Simonetti, 2011; Swan *et al.*, 2017). For instance, tigers have been reintroduced to 'rewild' Protected Areas [e.g. Satkosia and Panna Tiger Reserves in India (Vasudeva *et al.*, 2021; Malviya, Kalyanasundaram & Krishnamurthy, 2022)], and following human/livestock depredation events leopards have frequently been translocated from human-use areas to forest habitats (Athreya *et al.*, 2011, 2015). There are plans to reintroduce dholes into Protected Areas in India where they have recently gone extinct (Jhala *et al.*, 2021). Such interventions seldom consider competition and population-level interactions amongst species. Our findings make a strong case for wildlife managers to acknowledge and evaluate these aspects prior to implementing actions.

(8) Our predictions on intraguild competition, conspecific competition and livestock depredation hinge on reliable estimates of predator (and prey) population densities. This information remains prominently missing for dholes, because of the field, logistical, and methodological challenges associated with estimating their numbers (Kamler *et al.*, 2015). Recent studies are filling this gap and slowly improving dhole population estimates using novel methods (Ngoprasert, Gale & Tyre, 2019; Srivathsa *et al.*, 2021; Punjabi *et al.*, 2022). The magnitude of intraguild competition, as well as potential levels of livestock depredation predicted in our study may need to be recalibrated when information on dhole population sizes becomes available from various locations across their distribution range.

(9) The literature on negative interactions between humans and carnivores, usually linked to livestock depredation, is now abundant (see Lozano *et al.*, 2019; Venumière-Lefebvre, Breck & Crooks, 2022). We show how wild prey availability and intraguild coexistence could potentially have collateral effects on conspecific competition, with consequences for livestock depredation. Empirically testing and comparing levels of livestock depredation (or 'conflict') across locations may be difficult because there is no standard metric available for undertaking such an evaluation. We posit that formulating and implementing a uniform framework to quantify livestock losses across sites would provide useful information for future analyses.

(10) Ecological crises like species extinctions and biodiversity collapse across the tropics of the Global South often focus research efforts on applied aspects that proximally and tangibly benefit wildlife protection efforts (Wilson *et al.*, 2016). In this context, most studies tend to be biased towards mammalian carnivores, treating them as sentinels of ecosystem health and functioning (Sergio *et al.*, 2006, 2008). Our study shows how insights gained from fundamental ecology in terms of behaviour, diet, intraguild competition, and associated networks of interactions can substantially augment our understanding of carnivore ecological requirements, and thereby better inform strategies for their conservation and management.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

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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. List of data sources used in the analyses.
Appendix S2. Summary list of study locations and corresponding category/categories for which information from these sites was used in the analyses.
Appendix S3. Scores and estimates for direct dyadic interactions.
Appendix S4. Population-level interactions between dholes (D), leopards (L) and tigers (T).
Appendix S5. Calculations of prey biomass consumed (% of total diet) by dhole (S5a), leopard (S5b) and tiger (S5c) across study site locations.

Appendix S6. Summary of wild ungulate prey biomass, livestock biomass and total prey biomass consumed by dhole, leopard and tiger across study site locations over a 12-month period.

Appendix S7. Ungulate prey densities, tiger density and leopard density across 40 Protected Areas in India.

Fig. S1. Relative proportions of wild ungulate prey biomass consumed by dholes, leopards and tigers in 15 locations across Asia.

Fig. S2. Spatial interaction factor (SIF; $N = 16$) and temporal interaction factor (TIF; $N = 19$) for leopard–tiger interactions across 18 locations.

Fig. S3. Prey biomass available (PBA) and spatial interaction factor (SIF) or temporal interaction factor (TIF) for leopard–tiger interactions at seven locations for which information was available.