



Every dog has its prey: Range-wide assessment of links between diet patterns, livestock depredation and human interactions for an endangered carnivore



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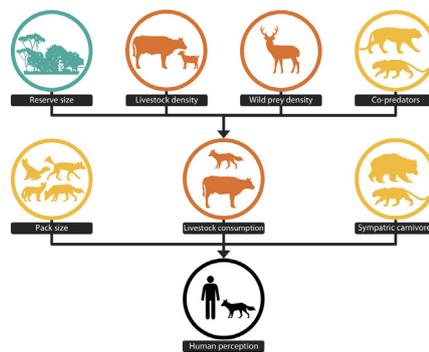
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HIGHLIGHTS

- We compared levels of wild and domestic prey consumed by dholes using data from all published studies across its range
- Meta-analysis revealed that livestock consumption was influenced by wild and domestic prey, and number of co-predators
- People's perception of dholes was shaped by pack sizes, levels of livestock depredation and number of sympatric carnivores
- Global carnivore conservation strategies should incorporate regional realities, ecological contexts and human perceptions

GRAPHICAL ABSTRACT



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ABSTRACT

Livestock depredation is the most ubiquitous type of negative interaction between humans and carnivores. We conducted a range-wide assessment linking diet patterns of the endangered dhole *Cuon alpinus*, with livestock consumption and human–dhole interactions. We first performed a reanalysis of dhole diet data from all published studies (1973–2013) incorporating a recently-developed non-linear correction factor for quantifying prey biomass consumed. We then determined the relative livestock numbers consumed by dholes over time across its range, compared these with earlier estimates, and investigated the relative importance of wild vs. non-wild prey in dhole diet. Using information from >70 studies, we explored links between livestock consumption by dholes, availability of wild versus non-wild prey, sympatric depredation-prone carnivores, and people's perception of dholes as livestock predators. We found that (a) dhole diet profiles varied regionally, (b) dholes consumed fewer livestock compared to estimates generated using other, widely used methods, (c) livestock consumption by dholes was associated with wild and non-wild prey densities, and number of co-predator species, and (d) people's negative perception of dholes was associated with pack sizes, levels of livestock depredation and number of sympatric carnivore species. Global efforts for dhole conservation should involve different strategies based on region-specific realities that account for ecological context as well as human perceptions, which

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would require well-designed studies of dhole social and population dynamics, and human–dhole interactions. We also call for more such range-wide assessments of livestock depredation by wild canids, complemented with direct investigations of human–canid interactions.

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1. Introduction

Global increase in the spatial overlap between humans and large mammalian carnivores presents several conservation challenges (Ripple et al., 2014). Among the key issues with increased human–carnivore interface is the loss of human lives and livelihoods. These damages generally pertain to livestock depredation and perceived threat to human safety or property. Attacks on humans resulting in serious injuries or fatalities represent a very small proportion on the negative extreme of the human–wildlife interaction spectrum (Quigley and Herrero, 2005). Wildlife managers and conservation biologists have long been interested in understanding negative interactions between humans and large carnivores in an attempt to reduce wildlife-related losses, while also enabling persistence of carnivore populations (Treves and Karanth, 2003). Given that livestock depredation by carnivores remains the most ubiquitous type of damage (Van Eeden et al., 2018a), ascertaining levels and economic consequences of depredation, and exploring ways to mitigate such losses are important for carnivore conservation.

The complex nature of human–carnivore interactions manifests in local and regional peculiarities. In certain countries and regions, the mere presence of carnivores in human-use areas may be viewed as a negative interaction (Wilson et al., 2006). On the other hand, countries with human acceptance of large carnivores in ‘conservation-enabled’ landscapes have allowed the latter to thrive in shared spaces (Athreya et al., 2015). Carnivore species that are perceived to pose a threat to human life and property generally suffer from exaggerated negative attitudes from people, although the economic damages they inflict may be low or negligible (Kolipaka et al., 2015). In such cases actual losses are substantially lower than perceived losses (Agarwala et al., 2010). These perceptions are further compounded by hidden opportunity or psychological costs (Madden and McQuinn, 2014). Wildlife managers and conservationists intending to foster persistence of carnivore populations and reduce their negative interactions with people can benefit from identifying and incorporating region-specific social attributes that form the backdrop of these interactions (Chapron and López-Bao, 2014; Dickman et al., 2014). There is need, therefore, to understand associations between levels of carnivore-related losses, causes of livestock depredation and people’s negative perception of carnivores.

Most studies that examine human–carnivore interactions are site-specific and descriptive, and seldom delve into experimental or quasi-experimental assessments (Miller, 2015). While information generated by such studies is important from a local management standpoint, they fall short of identifying broader patterns that could inform regional-, national- or global-level policies (Treves and Karanth, 2003; Can et al., 2014; Holland et al., 2018). In this context, systematic reviews, range-wide meta-analyses or syntheses hold certain potential to provide novel insights. For example, a global review by Inskip and Zimmermann (2009) identified key gaps in studies of human–felid interactions. Khorozyan et al. (2015) present a meta-analysis of large felid depredation on livestock and the role of wild prey in affecting this interaction. Using information from multiple countries and species, Packer et al. (2018) explored attributes associated with spatio-temporal intensities of human attacks by large felids. Global-scale syntheses by Eklund et al. (2017) and Van Eeden et al., 2018b further emphasize the need for evidence-based strategies in mitigating carnivore-related livelihood losses. Such analyses have pruned our perspectives on the intricacies that link people, predators and policy.

Investigating diet profiles can provide insights on livestock depredation by carnivores, and allow for gauging the extent of their dependence on non-wild prey (Marker et al., 2003; Kolipaka et al., 2017). Examining diet patterns using prey remains in fecal matter (scats) has been the cornerstone of carnivore ecology and natural history studies (e.g., Floyd et al., 1978; Ackerman et al., 1984; Putman, 1984; Carbone et al., 1999). Over time, development of novel analytical frameworks and application of genetic methods have improved the reliability of such assessments (Carreon-Martinez and Heath, 2010; Klare et al., 2011). For nearly three decades, ecologists used a correction factor that assumes a linear relationship between prey body mass and biomass consumed by carnivores (see Floyd et al., 1978 for canids; Ackerman et al., 1984 for felids). Recently, Wachter et al. (2012) proposed a more realistic non-linear relationship between the two, based on feeding trials of carnivores in captivity. Subsequent studies that have built upon and applied this non-linear correction factor show significant disparities between results from the two methods (Chakrabarti et al., 2016; Lumetsberger et al., 2017). These findings call for a reassessment of carnivore diet profiles to better understand the consequences of their dependence on wild versus non-wild prey.

Global patterns and trends in conservation assessments linking large carnivores and human interactions are generally biased, with very few studies focused on species and countries in the global south (see Wilson et al., 2016; Tensen, 2018). Given the urgency for formulating and implementing conservation actions, particularly for threatened or endangered carnivores, there is imperative need to undertake such investigations on species and in locations that are under-represented in literature. In this study, we perform a range-wide assessment of diet profiles of the endangered dhole *Cuon alpinus*, and link these with livestock consumption patterns and human–dhole interactions. We first performed a reanalysis of dhole diet from all published studies incorporating the non-linear correction factor proposed by Wachter et al. (2012). Based on this reassessment, we determined the relative numbers of livestock consumed by dholes over time and across the species’ geographic range, compared these with estimates generated using the older method, and investigated the relative importance of wild vs. non-wild prey. Using information extracted from >70 studies, we explored links between livestock consumption by dholes, availability of wild versus non-wild prey, sympatric depredation-prone carnivores, and people’s perception of dhole as a livestock predator. We draw on the results to discuss how differences in these links can inform region-specific management strategies for the endangered carnivore across its range.

2. Methods

2.1. Study species

Dholes are social carnivores that inhabit forests of south and south-east Asia (Kamler et al., 2015). The Red List assessment by the IUCN suggests that India harbors the largest population of dholes; Thailand and Myanmar support medium populations, whereas Bhutan, Cambodia, China, Indonesia, Laos, Malaysia and Nepal support small populations (Kamler et al., 2015). Over the past five decades, most ecological studies of dhole have dealt with diet analyses and behavioral observations (Johnsingh, 1982; Venkataraman et al., 1995; Karanth and Sunquist, 2000; Kumara et al., 2004; Ghaskadbi et al., 2016; see Supplementary information 1 for a full list of diet studies). More recently, select studies

have examined distribution and habitat associations at various spatial scales (Karanth et al., 2009; Jenks, 2012; Srivathsa et al., 2014; Punjabi et al., 2017). These studies suggest that, though generally restricted to forested wildlife reserves, dholes also use unprotected secondary forests, multi-use forest fragments, and agroforests adjoining protected reserves for movement and dispersal (Kumara et al., 2004; Srivathsa et al., 2014; Gangadharan et al., 2016). Further, since dholes are also shy and elusive, they do not frequently interact with humans. Although livestock depredation by dholes is relatively rare, some studies (see Karanth et al., 2013; Aryal et al., 2015; Srivathsa et al., 2019), anecdotal information, and ad hoc observations indicate possible regional differences in the frequency and intensity of attacks.

2.2. Data sources and description

We searched peer-reviewed scientific articles and book chapters through Google Scholar (www.scholar.google.com) and ISI Web of Science (www.webofknowledge.com) using the key words “dhole” and “cuon alpinus” in conjunction with different combinations of “diet”, “scat(s)”, “livestock”, and “prey”. We also scanned field guides and natural history books to locate older articles that were not digitally archived. Our search revealed 28 studies with 29 assessments of dhole diet in 19 locations (all within protected wildlife reserves) across 7 countries (Fig. 1) over the past 40 years (1974 to 2013). These articles formed the core of our dataset, based on which all subsequent analyses were undertaken. We then followed a snowball sampling approach (sensu Handcock and Gile, 2011), using references within these articles to retrieve ancillary data related to prey densities, size of protected reserves, list of carnivore species, livestock depredation reports, dhole pack sizes and human perceptions. We used the aforementioned data from studies whose assessment year was closest to the year in which the corresponding diet study was carried out in any given site. Livestock numbers and densities were obtained from the most temporally

proximate government census records of the respective countries. In certain cases where no published data or estimates were available for any of the variables described above, we obtained information by contacting local park officials or wildlife biologists (Table 1; Supplementary information 2 has detailed description of data and data sources).

2.3. Analytical methods

2.3.1. Diet analysis

Based on feeding trials with captive wolves, Floyd et al. (1978) proposed a linear relationship between prey body mass and prey biomass consumed per collectible scat:

$$Y = 0.035 + 0.020X \quad (1)$$

Eq. (1) assumes a linear relationship between prey body mass (X) and biomass consumed per collectible scat (Y). In reality, there is an upper bound beyond which an increase in prey biomass no longer translates into higher consumption, as determined by the carnivore's body size and feeding limits. Wachter et al. (2012) proposed a non-linear formulation of this relationship, accounting for maximum consumable biomass after which the regression line asymptotes.

$$Y = 1.382 (1 - \exp(-0.021X)) \quad (2)$$

We first compiled body mass values for each prey species as average weights of adult females from multiple published literature, field guides and other sources (Supplementary information 3). To account for variation within species age/size classes, we used 0.75 times the average adult female body mass (X) in our analyses (Jooste et al., 2013; Zhang et al., 2013). We set the upper bound of prey body mass to 200 kg (see Hayward et al., 2014). Using these values of X, we computed species-specific correction factor Y from Eqs. (1) and (2). For each diet

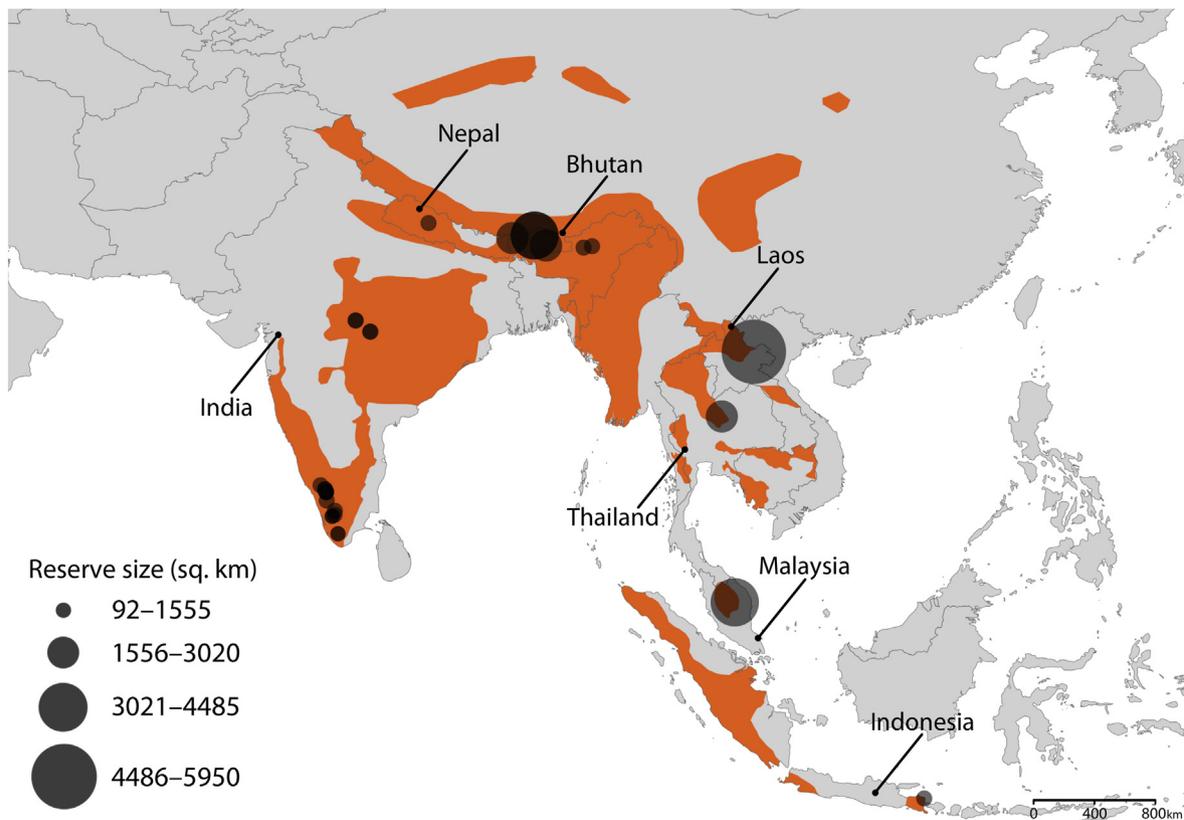


Fig. 1. Map of dhole distribution range (based on IUCN Red List assessment, 2015) and locations of sites where diet studies were conducted (1974 to 2013). Reserve size refers to the size of the protected reserve (at present) where studies were conducted.

Table 1
Details of 29 diet assessments and associated ancillary information from >70 studies on dholes, co-predators, prey and human–dhole interactions (1974 to 2013). Study area size refers to the extent of area sampled, as mentioned in the corresponding study. Reserve size is the size of protected reserve where the study was conducted. Sympatric carnivores are mid- to large-sized carnivores that co-occur with dholes in the same protected reserve or study location. Co-predators are carnivores that likely compete with dhole for the same prey species. Negative perception is based on people's perception of dholes – '1' indicates high livestock losses attributed to dholes, and '0' indicates negligible or no livestock loss attributed to dholes.

Location (code)	Year(s) of study	Study area (km ²)	Reserve size (km ²)	No. of sympatric carnivores	No. of co-predators	Ungulate prey density (/km ²)	Avg. pack size	Livestock density (/km ²)	Negative perception (Y/N)
Mudumalai, India (MM1)	1974	321	321	5	3	46.02	5	195.77	Y
Mudumalai, India (MM2)	1975	321	321	5	3	46.02	5	195.77	Y
Mudumalai, India (MM3)	1975	62	321	5	3	46.02	5	195.77	Y
Mudumalai, India (MM4)	1988–91	130	321	5	3	46.02	8	195.77	Y
Mudumalai, India (MM5)	1989–93	321	321	5	3	46.02	8	195.77	N
Mudumalai, India (MM6)	2008–10	187	321	5	3	55.40	8	234.22	N
Bandipur, India (BP1)	1976–78	20	880	5	3	56.50	8.3	146.39	N
Bandipur, India (BP2)	2006	880	880	5	3	35.20	8.3	159.24	N
Eravikulam, India (EK)	1979–81	97	97	4	3	32.9	7.4	108.18	N
Nagarahole, India (NH)	1986–90	104	644	4	3	65.80	7	146.39	N
Parambikulam, India (PR)	2002–03	275	275	4	3	73.91	15	87.61	N
Anamalai, India (AM)	2001–04	958	958	5	3	73.91	15	90.50	N
Kalakad-Mundanthurai, India (KM)	2010	900	900	4	3	11.9	–	136.36	N
Silent Valley, India (SV)	2011–12	48	92	4	3	13.12	7	64.60	N
Pench landscape, India (PN1)	2001–04	292	758	6	4	63.80	7.5	238.57	N
Pench, India (PN2)	2006–11	410	410	6	4	63.80	13.9	44.20	N
Satpura, India (SP1)	2002–06	200	1428	5	3	14.40	8	48.01	N
Satpura, India (SP2)	2005	336.7	1428	5	3	14.40	8	48.01	N
Pakke, India (PK1)	2009–11	862	862	4	5	15.12	2	21.40	Y
Pakke landscape, India (PK2)	2011–12	10,000	862	4	5	15.12	2	33.84	Y
Khangchendzonga, India (KZ)	2008–10	182	2620	4	6	5.45	4.3	20.88	Y
Dhorpatan, Nepal (NP)	2012	1325	1325	5	5	16.00	5	85.92	Y
Jigme Singye, Bhutan (BT1)	2004–08	1723	1723	4	6	7.04	8.3	5.06	Y
Jigme Dorji, Bhutan (BT2)	2009 dry	50	4349	6	7	7.04	11.6	6.47	N
Jigme Dorji, Bhutan (BT3)	2009 wet	50	4349	6	7	7.04	11.6	6.47	Y
Phu Khieo, Thailand (TL)	2000–02	1560	1560	3	5	5.70	6.5	8.31	N
Taman Negara, Malaysia (MY)	1999–01	600	4343	3	4	10.33	3	8.47	N
Nam Et-Phou Louey, Laos (LS)	2005–10	5950	5950	4	5	5.29	–	7.82	N
Baluran, Indonesia (ID)	2013	250	250	1	1	17.40	10	172.66	N

MM1 - Fox and Johnsingh (1975); MM2 - Cohen et al. (1978); MM3 - Barnett et al. (1980); MM4 - Varman and Sukumar (1993); MM5 - Venkataraman et al. (1995); MM6 - Ramesh et al. (2012a); BP1 - Johnsingh (1983); BP2 - Andheria et al. (2007); EK - Rice (1986); NH - Karanth and Sunquist (1995); PR - Joseph et al. (2007); AM - Kumaraguru et al. (2010); KM - Selvan et al. (2013a); SV - Dar and Khan (2016); PN1 - Acharya (2007); PN2 - Majumder (2011); SP1 - Edgaonkar (2008); SP2 - Borah et al. (2009); PK1 - Selvan et al. (2013b); PK2 - Lyngdoh et al. (2014); KZ - Bashir et al. (2014); NP - Aryal et al. (2015); BT1 - Wang and Macdonald (2009); BT2 - Thinley et al. (2011); BT3 - Thinley et al. (2011); TL - Grassman et al. (2005); MY - Kawanishi and Sunquist (2008); LS - Kamler et al. (2012); ID - Nurvianto et al. (2016). List of references for these studies are provided in Supplementary information 1.

study (Table 1), we obtained data on percentage occurrence of prey species in scats (A). The biomass of each prey species consumed (BM) was calculated as $BM = (A * Y)$ and expressed as percentage (%BM or relative biomass consumed). Similarly, numbers of each prey species consumed were calculated as $RN = (BM / X)$, expressed as percentage (%RN or relative number consumed).

2.3.2. Patterns of prey consumption

We divided the 19 study locations into four major regions (SI: South India, CI: Central India, NR: Northeastern Region, SEA: South-East Asia) to make comparisons of relative prey biomass and numbers consumed by dholes. For ease of interpretation, we classified prey species into four broad groups: ungulates, primates, small mammals and domestic livestock. In particular, we were interested in comparing %RN and %BM of livestock consumed, estimated from Eqs. (1) and (2). Given that dhole packs generally prey on medium- to large-sized species, we predicted that the linear correction factor would over-estimate %RN and %BM of livestock consumed.

2.3.3. Livestock consumption and people's perceptions

To understand the mechanisms that engender people's negative attitudes towards dholes, we followed a two-step process. First, we sought to determine potential explanatory variables associated with livestock predation by dholes. Since we could not directly make assessments of predation, we instead use livestock 'consumption' as a surrogate. For each study, we assigned a 1/0 (binary response variable) based on whether or not domestic livestock remains were found in the scats. We expected a negative influence of reserve size (size of the protected reserve) and ungulate density on livestock consumption,

because dholes would be less likely to risk human interactions (through depredation) when there is adequate space and wild prey-base. We expected a positive influence of livestock density and number of species of co-predators, because higher livestock availability and greater competition for wild prey could increase the probability of dhole predation on livestock.

In the second step, we modelled variables potentially associated with people's negative perception of dholes. Information on human perception was derived from surveys where people self-reported loss, or compensation claims in management records, or through interviews with local wildlife experts (see Supplementary information 2). Quantifying negative perception was not possible across studies/locations because there were no standard methods or metrics for reporting levels of livestock losses, depredation or negative interactions. We therefore followed the approach adopted by Khorozyan et al. (2015) and treated negative perception as a binary variable– we assigned '1' when there was high livestock losses attributed to dholes, and '0' when there was negligible or no livestock loss attributed to dholes. As predictors, we used average dhole pack size, livestock consumption (as binary variable 1/0, as well as a continuous variable %RM from the diet analysis using Eq. (2) described above), and number of sympatric carnivores. We expected that (a) people may view larger packs more negatively than they do smaller packs, (b) presence and proportion of livestock remains in dhole's diet would be positively associated with negative perceptions, and (c) people's perceptions of dholes would be more negative in sites with higher number of sympatric carnivores perceived to be dangerous (see Farhadinia et al., 2017).

The two-step process described above is presented schematically in Fig. 2. In both steps, we used generalized linear models with a logit link

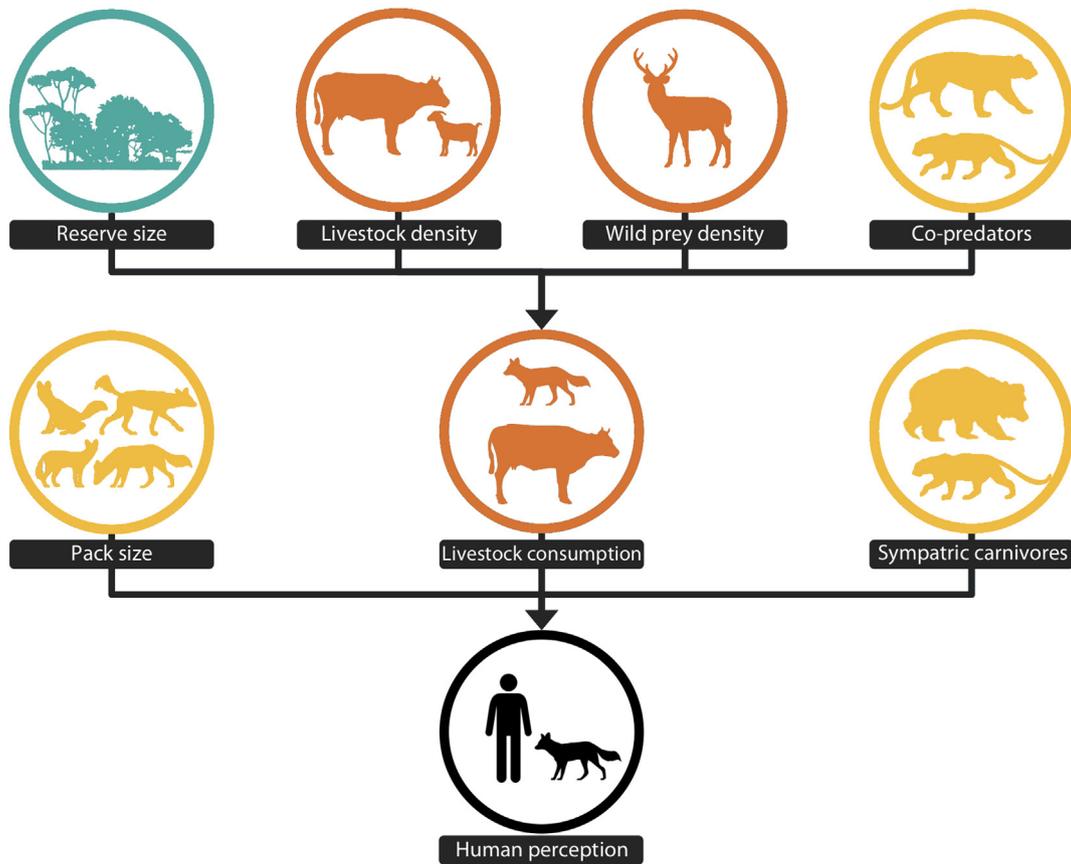


Fig. 2. Schematic representation of the two-step process linking livestock consumption by dholes and people's negative perception of dholes.

function to derive the relationship between response and predictor variables. All continuous predictors were z-transformed and screened for cross-correlations prior to analysis. We tested for the influence of singular, additive and interactive effects of predictors, and also compared these against an intercept-only model. To avoid overfitting, we used only up to two predictors in each model (three in the case of interactive effects; Tables 2 and 3). Model fits were compared using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002), and the influence of predictors was gauged based on magnitude, direction and statistical significance of corresponding β -coefficients. All analyses were performed in program R (R Core Team, 2014).

3. Results

We compiled information from a total of 8249 scats (range = 33 to 2074 per study; Supplementary information 2). Across 29 studies, dhole

diet consisted of 50 prey items in total, 41 of which were used here for analysis of relative biomass and relative numbers consumed (vegetative material, invertebrates and small birds/reptiles were excluded). The number of prey species consumed by dholes ranged from 2 to 12 per study, and mean number of prey species consumed was highest in south India to lowest in northeastern region (SI: 5.93, CI:5, NR: 4.3, SEA: 5.75; Supplementary information 3). Average pack sizes ranged from 2 to 15 (Table 1). Dholes shared space with 12 medium- to large-sized carnivore species across their distribution range; 10 of these were potential co-predators that competed for similar prey species (Table 1; Supplementary information 1).

3.1. Wild and non-wild prey consumption across regions

Relative biomass (%BM) and relative numbers (%RN) of prey consumed by dholes, estimated based the non-linear correction factor, are

Table 2

Model comparison to identify predictors influencing livestock consumption by dholes, based on 29 diet studies across dhole distribution range. The response variable is either 1 or 0, denoting presence or absence of livestock remains in dhole scats. K = number of parameters.

Model ID	Models	K	AICc	Δ AICc	Model likelihood	AICc weight	Log-likelihood	Cumulative weight
D1	ungulate density	2	38.66	0.00	1.00	0.31	-17.10	0.31
D2	copredators + ungulate density	3	39.51	0.86	0.65	0.21	-16.28	0.52
D3	reserve size + ungulate density	3	40.81	2.15	0.34	0.11	-16.93	0.63
D4	reserve size	2	40.93	2.28	0.32	0.10	-18.24	0.73
D5	copredators \times ungulate density	4	41.10	2.44	0.29	0.09	-15.72	0.82
D6	livestock density	2	41.53	2.87	0.24	0.07	-18.53	0.90
D7	intercept	1	42.04	3.38	0.18	0.06	-19.95	0.95
D8	reserve size \times ungulate density	4	43.51	4.85	0.09	0.03	-16.92	0.98
D9	copredators	2	44.31	5.65	0.06	0.02	-19.92	1.00

Table 3
Model comparison to identify predictors influencing people's negative perception of dholes, based on 27 diet studies across dhole distribution range. Two studies (locations) where information on average pack sizes were not available have been excluded from analysis. Here, people's perception towards dholes is treated as a binary variable (0 = negligible or no livestock loss attributed to dholes; 1 = high livestock losses attributed to dholes). In the table, *livestock consumed* refers to a continuous variable (%RN) and *livestock consumed y/n* is a binary variable (1 = scat contained livestock remains, 0 = scat did not contain livestock remains). K = number of parameters.

Model ID	Models	K	AICc	Δ AICc	Model likelihood	AICc weight	Log-likelihood	Cumulative weight
C1	<i>pack size + livestock consumed</i>	3	30.21	0.00	1.00	0.33	-11.58	0.33
C2	<i>pack size + livestock y/n</i>	3	30.88	0.67	0.72	0.24	-11.92	0.57
C3	<i>pack size + sympatric carnivores</i>	3	31.58	1.37	0.50	0.17	-12.27	0.74
C4	<i>pack size</i>	2	32.68	2.47	0.29	0.10	-14.09	0.84
C5	<i>pack size \times livestock consumed</i>	4	32.88	2.68	0.26	0.09	-11.53	0.93
C6	<i>pack size \times sympatric carnivores</i>	4	34.36	4.15	0.13	0.04	-12.27	0.97
C7	<i>livestock y/n</i>	2	37.11	6.91	0.03	0.01	-16.31	0.98
C8	<i>intercept</i>	1	37.75	7.55	0.02	0.01	-17.80	0.99
C9	<i>livestock consumed</i>	2	38.65	8.44	0.01	0.01	-17.07	0.99
C10	<i>sympatric carnivores + livestock y/n</i>	3	39.57	9.36	0.01	0.00	-16.26	0.99
C11	<i>sympatric carnivores</i>	2	39.79	9.59	0.01	0.00	-17.65	1.00
C12	<i>sympatric carnivores + livestock consumed</i>	3	40.65	10.44	0.01	0.00	-16.80	1.00
C13	<i>sympatric carnivores \times livestock y/n</i>	4	42.33	12.12	0.00	0.001	-16.25	1.00
C14	<i>sympatric carnivores \times livestock consumed</i>	4	42.68	12.47	0.00	0.001	-16.43	1.00

presented in Fig. 3. Relative biomass consumed by dholes was higher for primates in southeast Asia and for livestock in northeastern region.

In terms of relative numbers, dholes appeared to consume more primates in central India (compared to other sites), higher number of small mammals in southeast Asia and higher numbers of livestock in northeastern region (see Fig. 3). Differences in estimates of %BM and %RN based on linear and non-linear equations showed that the former overestimated the role of small prey ($X < 7$ kg) and underestimated the role of medium-sized prey ($X = 7-70$ kg; Supplementary information 4). Livestock remains were reported in 16 of 29 assessments, with percentage occurrence ranging from 0.28% in Pench to 13.5% in Bhutan. Smaller livestock (goats and sheep) were recorded in 3 studies and large livestock in 15 studies. We compared estimates of livestock consumption based on Eqs. (1) and (2) using Wilcoxon signed rank test. The linear Eq. (1) almost consistently overestimated %BM ($V =$

128, $p = 0.001$) and %RN ($V = 121$, $p = 0.004$) of livestock consumed, compared to those generated using Eq. (2). Site-wise values of %BM and %RN computed using Eqs. (1) and (2) are presented in Fig. 4.

3.2. Linking livestock consumption and human perceptions

We used presence or absence (1/0) of livestock remains in scats to indicate livestock consumption by dholes. We constructed 9 models representing *a priori* predictions and compared their relative fits to identify variables influencing livestock consumption (Table 2). Six models containing covariates performed better than the intercept-only model, and the top two models had comparable statistical support (Δ AICc < 2). These models included singular effect of ungulate density, and an additive effect of ungulate density and number of co-predators. The β -coefficients indicated a positive effect of ungulate density,

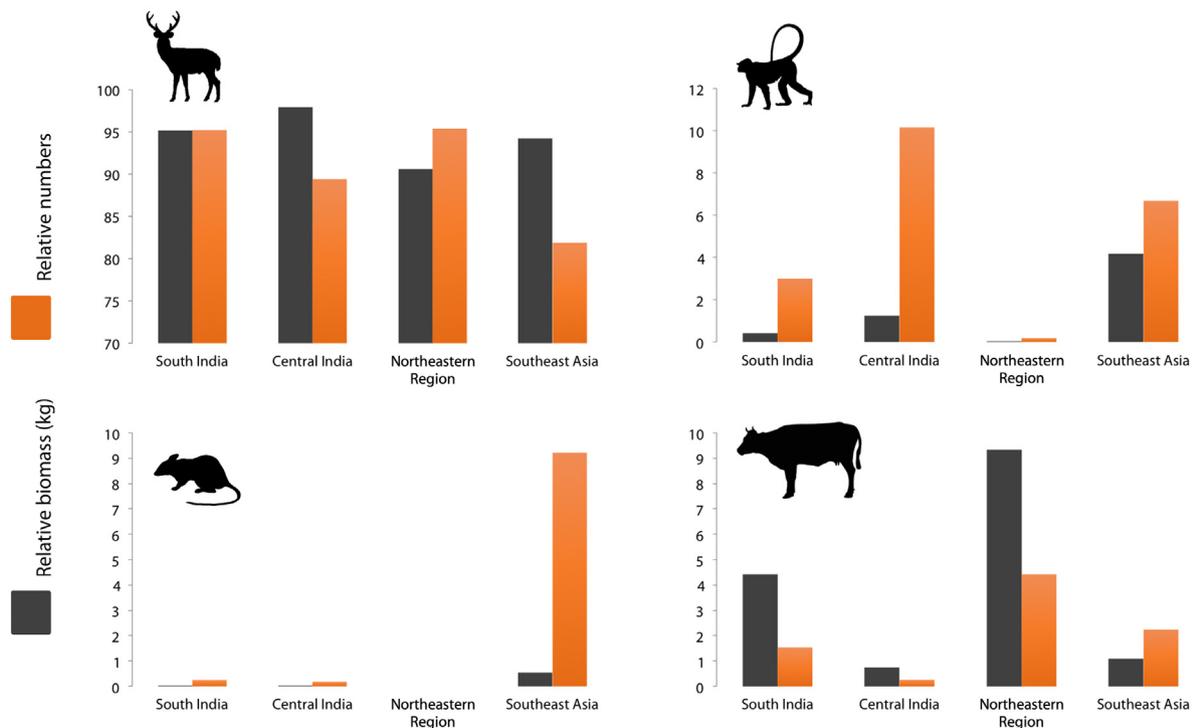


Fig. 3. Region-wise estimates for relative biomass (%BM) and relative numbers (%RN) of prey consumed by dholes; prey species classified into four ecologically relevant groups: ungulates (top left), primates (top right), small mammals (bottom left) and domestic livestock (bottom right).

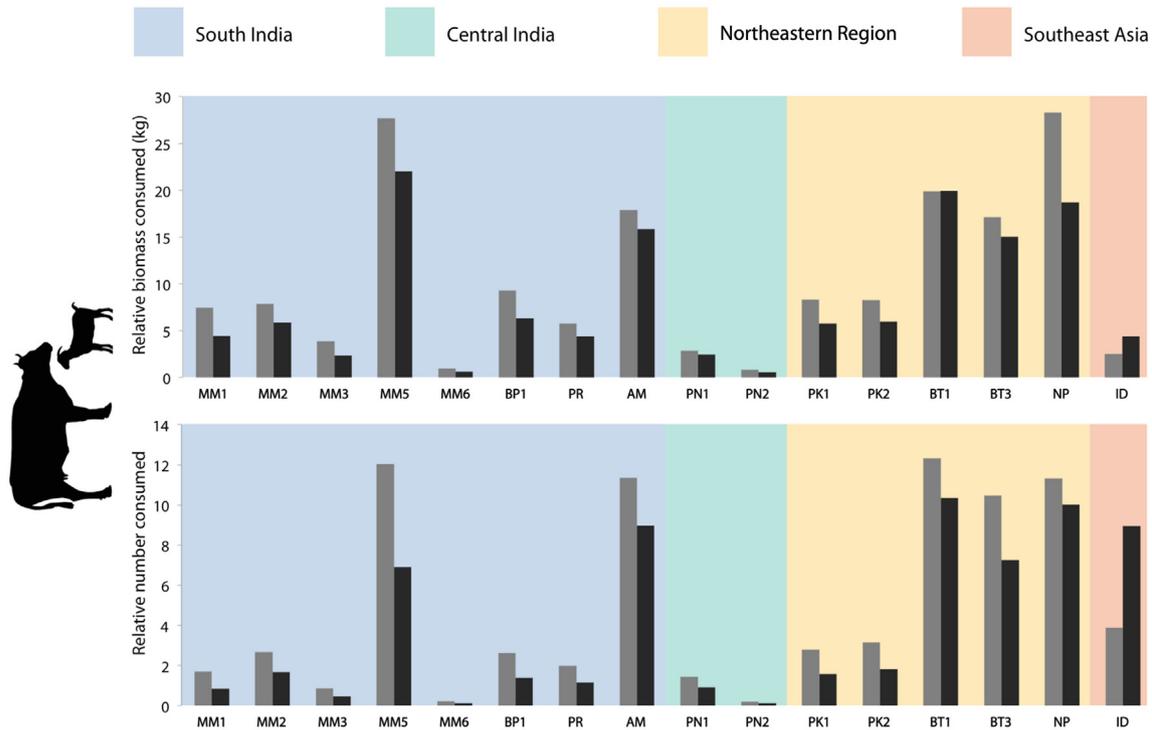


Fig. 4. Study-specific comparisons of relative biomass (%BM) and relative numbers (%RN) of livestock consumed by dholes. Estimates are from linear (old; light grey bars) and non-linear (new; dark grey bars) correction factors. Individual study sites are along the x-axis (see Table 1 for site name and year of study).

number of co-predators and livestock density, and a negative effect of reserve size on livestock consumption by dholes (Table 4). We note that the latter three received relatively weak statistical support (95% confidence intervals straddled 0).

In the second step, we treated people’s perception towards dholes as a binary response variable (0 = negligible or no livestock loss attributed to dholes, 1 = high livestock losses attributed to dholes), and tested for the effect of a set of potential variables influencing these perceptions. We compared 13 covariate models and the intercept-only model for identifying determinants of people’s perception towards dhole. Seven models with covariates or covariate combinations ranked higher than the null model (Table 3). The top-ranked model included an additive effect of pack size and relative number of livestock consumed, although two other models that included pack size as a predictor received comparable support (based on AICc scores). Average pack size had a strong negative effect (smaller packs more likely to be viewed negatively); livestock consumption (0/1 and %RN consumed) and number of sympatric carnivores had a positive effect on people’s negative perception (Table 4).

4. Discussion

Agricultural intensification and expansion of commodity land-use for livestock husbandry tip the scales heavily in favor of a burgeoning human population (Baker et al., 2008; Dobrovolski et al., 2013; Ripple et al., 2014). Making room for wildlife, particularly large carnivores, therefore presents many challenges. Negative interactions between humans and large carnivores further complicate carnivore conservation in rapidly changing landscapes (Treves and Karanth, 2003; Treves et al., 2016). Given this background, an understanding of mechanisms that accentuate or mediate consequences of human–carnivore interface is of importance for wildlife managers and conservationists. Our meta-analysis showed that livestock consumption by dholes was correlated with densities of wild and non-wild prey, and possibly, the number of competing co-predator species. Human perceptions, specifically negative attitudes towards dholes, were shaped by pack sizes, while levels of livestock depredation and the number of sympatric large carnivore species had some effect (with lower statistical support).

Table 4

Estimates of β -coefficients (standard errors in parentheses) for predictor variables associated with livestock consumption by dholes, and people’s negative perception of dholes. Estimates presented for predictors are from corresponding models when they first appear in the candidate set, based on AICc ranks. Here, *livestock consumed* refers to a continuous variable (%RN) and *livestock consumed y/n* is a binary variable (1 = scat contained livestock remains, 0 = scat did not contain livestock remains).

		Intercept (SE)	β (SE)	Non-interactive terms	Model ID
Livestock consumption	<i>ungulate density</i>	0.29 (0.42)	1.01 (0.47)**	–	D1
	<i>co-predators</i>	0.31 (0.44)	0.64 (0.52)	–	D2
	<i>reserve size</i>	0.26 (0.43)	–0.31 (0.54)	–	D3
	<i>co-predators × ungulate density</i>	1.44 (1.37)	2.00 (2.21)	2.52 (2.25); 2.48 (1.46)*	D5
	<i>livestock density</i>	0.24 (0.39)	0.67 (0.42)	–	D6
Negative perception	<i>pack size</i>	–0.92 (0.56)	–2.13 (0.88)**	–	C1
	<i>livestock consumed</i>	–0.92 (0.56)	1.25 (0.65)*	–	C1
	<i>livestock consumed (y/n)</i>	–2.04 (0.91)	2.10 (0.92)*	–	C2
	<i>sympatric carnivores</i>	–1.13 (0.61)	1.49 (0.92)	–	C3
	<i>pack size × livestock consumed</i>	–1.03 (0.68)	0.27 (0.84)	–2.19 (0.91); 1.20 (0.64)	C5
	<i>pack size × sympatric carnivores</i>	–1.13 (0.70)	0.01 (0.82)	–2.29 (0.97); 1.49 (0.98)	C6

* $p < 0.10$.
 ** $p < 0.05$.

Prey consumption patterns by dholes showed regional differences (Fig. 3). Consumption of wild ungulates was highest in south and central India, perhaps reflecting high abundance of this prey group (Karanth et al., 2004). The northeastern region, in contrast, had the highest levels of livestock consumption. This may be attributed to very low densities or absence of large-sized ungulates in the region, owing to a history of extensive hunting (Datta et al., 2008; Velho et al., 2012). Application of robust analytical methods for diet assessments are important while gauging wild carnivores' dependence on non-wild prey, as it can have serious socio-economic and political ramifications (see Boast et al., 2016). For instance, Chakrabarti et al. (2016) found that economic losses due to livestock depredation by Asiatic lion *Panthera leo* in western India were lesser than estimates derived from older methods (Meena et al., 2011). By demonstrating that dholes consume much fewer livestock prey than estimates generated using the older linear equation (see Fig. 4), our results address a critical gap in the current understanding of human–dhole relationship.

Livestock depredation is generally a consequence of intricate interplay between densities of wild prey, livestock and carnivores, in combination with husbandry practices, and landscape and habitat features (Montgomery et al., 2018). Wild prey populations often serve as mediating factors, where higher densities decrease chances of livestock depredation by carnivores (Meriggi and Lovari, 1996; Ghoddousi et al., 2016). Contrary to our expectation, we found a positive effect of wild prey densities on livestock consumption by dholes. But we also found a positive interactive effect of wild prey densities and number of co-predator species on livestock consumption (model support for which was indicative, but not statistically significant). We suspect these results likely indicate an indirect interaction, wherein high levels of competition for wild prey may coerce dholes into consuming more non-wild prey. Nonetheless, since the associations were suggestive rather than conclusive, our results provide opportunity for exploring these predictions in other species and systems with wider, more extensive literature.

The role of people's attitudes and perceptions, and their acceptance of wildlife have facilitated co-existence in shared spaces (Goodale et al., 2015; Vucetich et al., 2015). These factors, however, cannot be considered in isolation because in many cases there are mismatches between people's perceptions and reality (Agarwala et al., 2010; Kolipaka et al., 2015). In our case, probability of negative perception seemed to closely mirror ground realities; people were more likely to view dholes as depredators when they consumed more livestock. These results corroborate findings by Miller et al. (2016) who found similar trends with large felids in central India. People also seemed to view dholes more negatively in locations where average pack sizes were smaller, which may support the hypothesis that larger packs are less likely to risk interactions with humans. Although dholes consumed livestock in all regions, negative attitudes appeared to be higher in the northeastern region. A legacy of cultural reverence (Karanth et al., 2013), human acceptance or indifference (Srivathsa et al., 2019), and in some cases, using dholes to procure wild meat through kill-stealing (Kumara et al., 2004) may form the basis for such regional differences in attitudes. We do note however that our treatment of the 'perception' variable was somewhat simplistic; a standardized and quantified metric of human perceptions would certainly provide a more lucid understanding of these interactions.

Mitigating human–carnivore conflicts is veritably complex, and cannot benefit from blanket strategies based on ecological perspectives of predator–prey relationships alone (Treves et al., 2016; Redpath et al., 2017). Persistence of carnivore populations within and beyond protected reserves will depend on how their interactions with humans are managed, particularly in areas where people view them negatively (Bruskotter and Wilson, 2014). Northeast India, Nepal and Bhutan, for instance, have had a long history of rampant persecution of dholes (Mishra et al., 2006; Katel et al., 2014; Lyngdoh et al., 2014). Wildlife managers often mull culling as an option to control dhole populations,

which has proved disastrous for ecological balance in the past (Wangchuk, 2004). Akin to the 'extinction debt' with some species, dholes appear to suffer from a 'perception debt' in the region, whereby historical negative perceptions continue to fuel current management attitudes and practices. Based on the results presented above, and insights from all the studies reviewed here, we posit that global efforts for dhole conservation may benefit from prioritizing (1) efficiency in dispensing monetary compensation for livestock losses in south and central India (Karanth et al., 2018), (2) investment in better husbandry practices, implementing insurance schemes and education programs in the north-eastern region (see Khatiwada et al., 2011), and (3) recovery of wild prey populations in southeast Asian reserves.

Although our study presents the first range-wide synthesis linking dhole diet, livestock depredation and people's perception, we acknowledge certain caveats in our approach. First, we were constrained by the limited number of dhole diet assessments and studies reporting ancillary data. Second, the methods for estimating prey densities have evolved over time, and the information from some of the older studies used here are 'guesstimates' at best. Third, sample sizes in diet studies ranged from 33 to 2074 scats, with varying survey effort. The sample size in some studies may have been too small for detecting all prey species in the diet profile (see Doherty et al., 2015), and some of our results may be biased. Fourth, studies considered here relied on ocular and morphometric methods to identify dhole scats and to ascertain prey species in scats; we cannot discount the fact that there may have been misidentification of species. Application of genetic methods (Klare et al., 2011; Morin et al., 2016) in the future can reduce potential errors arising from the same. Finally, carnivore population size is an important component for understanding the dynamics examined here, but this information does not exist for dholes. Future studies should prioritize estimation of dhole abundance to explicate this important knowledge gap.

5. Conclusion

Studies of carnivore diets can provide insights on prey preferences, behavioral adaptations, carrying capacities and intra-guild competition (Karanth and Sunquist, 1995; Weckel et al., 2006; Banerjee et al., 2013; Mengülluöglu et al., 2018). Meta-analyses that utilize such information can offer range-wide perspectives that improve our ecological understanding of species while also informing conservation and management. Review studies and syntheses pertaining to large felids (e.g., Inskip and Zimmermann, 2009; Khorozyan et al., 2015; Packer et al., 2018) have been of great utility in furthering our understanding of their interactions with humans. But studies of human–felid interactions far outnumber those of human–canid interactions (e.g., Newsome et al., 2016). It is important to amend this disparity through targeted assessments of wild canids in shared spaces, more so because the spatial overlap between humans and wild canids is considerably higher (Ripple et al., 2014). Although our study goes some distance in doing so with the dhole as focal species, we call for more such global assessments, supplemented by investigations of diet and human–canid interactions for other wild canid species.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.136798>.

Declaration of competing interest

The authors declare no conflict of interests.

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