

Diet and prey preferences of the dhole *Cuon alpinus*: dietary competition within Asia's apex predator guild

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Abstract

Group hunting predators theoretically benefit from hunting together through increased prey returns, however studies on lions suggest food is not enough. The dhole is one such group hunter, however its predatory role within Asia's large predator guild is less well known than other members. We tested whether dholes exhibit preferential predation, and determined the drivers of prey choice and whether pack size affected diet to ascertain the fundamental resources required for the species' conservation, given lack of a prey base is the primary threat to this species. We reviewed the literature and found 24 studies from 16 sites from throughout the species extant range that reported on 8816 records (scat + kills) of 19 species. Jacobs' index revealed that sambar *Cervus unicolor*, chital *Axis axis* and wild boar *Sus scrofa* contribute almost 2/3 of the food biomass of the dhole, with sambar being significantly preferred. Sambar are at the upper end of the accessible prey spectrum (30-235 kg), and marginally above the preferred weight range of 130 – 190 kg. The accessible prey spectrum extensively overlaps with leopards and tigers in Asia and reflects the extensive dietary competition within Asia's large predator guild, as tigers also preferentially prey on sambar

and leopard completely overlap in the accessible prey with dholes. Although prey preferences are not affected by pack size, larger packs ultimately take larger prey. This study documents for the first time the critical prey resources necessary for the conservation of dholes in Asia, and highlights the degree of competition potentially occurring across dhole distribution range.

Key words:

Competition, Large predators, group hunters, canids, south-east Asia, Sambar, Chital, wild pig, prey preference.

Introduction

Apex predators shape ecosystems and maintain trophic balance (Beschta & Ripple 2009, Ripple & Beschta 2012, Ripple *et al.* 2014). The dhole (*Cuon alpinus*) or Asiatic wild dog is one such large predator whose distribution is largely sympatric to that of tigers and leopards in the Asian continent (Durbin *et al.* 2008). However, unlike the tiger or leopard it has received much less of the ‘charismatic’ attention (Selvan *et al.* 2014, Selvan *et al.* 2013b, Johnsingh 1982, Bashir *et al.* 2014) and its role in Asia’s predator guild is poorly known beyond site specific studies.

The dhole is a terrestrial, pack-living canid that historically dominated large parts of alpine, temperate, tropical and sub-tropical forests of Asia (Durbin *et al.* 2008, Iyengar *et al.* 2005). Habitat fragmentation and several anthropogenic factors have limited the distribution of this large carnivore to a fraction of its historical range (Durbin *et al.* 2008, Cohen *et al.* 1978, Bashir *et al.* 2014). The current estimates of the dhole are of 2500 mature individuals and the primary threat of these is a loss of prey base, but this is poorly known at a species

level (Durbin *et al.* 2008). Few large carnivores may be as threatened as the dhole currently and the IUCN has recently re-classified the dhole as *Endangered* from *Vulnerable* on the Red List (Durbin *et al.* 2008). Retributive persecution due to alleged livestock depredation (Gopi *et al.* 2010, Gopi *et al.* 2012), poisoning and disease (Durbin *et al.* 2008, Davidar & Fox 1975) may be other important direct impacts on dhole populations worldwide.

The dhole is a cursorial hunter, known to be a voracious feeder that disembowels its prey (Johnsingh 1982). Snout injury or rump flank evisceration are common methods in killing of a prey by dholes (Johnsingh 1992, Karanth & Sunquist 2000). Hunting is usually by a chase led by any adult of the pack or by interception of the prey while being driven towards them. Hunting during nights is rare but may occasionally occur on moonlit nights (Johnsingh 1982). A successful hunt lasts for 13 -15 minutes and the prey is consumed immediately, since dholes do not cache their prey (Karanth & Sunquist 2000). Dhole usually consume roughly 2 kg/adult/day (Cohen *et al.* 1978, Johnsingh 1992, Fox 1984, Wang & MacDonald 2009). Thermoregulation influences daily activity of dholes, so they undertake high movements during the day and generally prefer to hunt during dawn or dusk (Venkataraman 1995).

Like African wild dogs *Lycaon pictus*, whose prey size may be significantly larger than their own body mass due to their group hunting strategy (Hayward *et al.* 2006b), dholes may hunt prey that are larger than their own body mass as they also hunt in groups. Dholes have a body mass (16 – 26 kg) that spans the 21.5 kg threshold of obligate carnivory (Carbone *et al.* 1999). Dholes may hunt a variety of prey ranging mainly from sambar *Cervus unicolor*, chital *Axis axis*, muntjac *Muntiacus muntjac* and wild pigs to even small prey such as hares *Lepus spp.* and porcupine *Hystrix indica* (Selvan *et al.* 2013a, Johnsingh 1992, Karanth & Sunquist 2000, Kumaraguru *et al.* 2011).

Prey preferred by dholes at individual sites is generally suggested to be medium-sized (Karanth & Sunquist 2000) while they are also said to hunt large prey (Wang & MacDonald 2009). Others suggest their preferred prey are deer, gaur *Bos frontalis*, banteng *B. javanicus* and other large bovids (Sillero-Zubiri 2009). Yet whether dholes are generalists within these weight categories or whether these specific preferences are supported more widely is unknown. Dholes and pi dogs (*pariah* dogs, *Canis familiaris*) hunt together occasionally but at kill sites, dholes have priority access (Davidar & Fox 1975). Even though high dietary overlap is seen with dhole diet to that of leopards and tigers at individual sites (Karanth & Sunquist 2000, Wang & MacDonald 2009, Andheria *et al.* 2007), little is known on the basis of their co-existence globally.

The aim of this paper was to determine whether dholes preferentially prey on particular prey species and identify what drives any such preferences. We tested (i) which large prey species are preferred/avoided and hence are crucial for the survival of the dhole? (ii) which prey are crucial for the dhole across its distribution range in different regions; (iii) whether pack size was related to larger prey taken or preferred; and (iv) what are the implications of this information for the conservation of this species?

Methods

Data on the diet of dholes was sourced from the literature via Google Scholar and Web of Science, and grey literature such as dissertations and the reference lists of those publications. We used data from the grey literature because these raw data were derived from standard, widely used analysis methods (scat analysis) and we made no use of any other methods, conclusions or inferences drawn within those reports (which are generally addressed in the peer-review process rather than the raw data provided robust methods are

used). We believe this is an appropriate use of grey literature and have used it previously (Lyngdoh *et al.* 2014). Furthermore, individual outlying studies are unlikely to bias our prey preference results because for a species to be significantly preferred or avoided several studies have to yield similar results (Hayward *et al.* 2006a).

Continuous observations are widely regarded as the superior method of ascertaining the diet of large predators (Mills 1992); however, these are extremely difficult with such wide-ranging, secretive and elusive predators as dholes and so all studies relied on scat analysis. This is likely to be biased towards prey at the smaller spectrum of dhole diet, however scats are likely to have been deposited by all members of dhole communities (i.e. both sexes and all age classes), so these factors are unlikely to bias our results.

Some study sites (Fig. 1) were repeatedly surveyed over several distinct time periods and these allowed temporally separated prey preferences to be calculated as prey abundance changed over time (Table 1). We used Jacobs' index to determine the prey selectivity of dholes:

$$D = \frac{(r_i - p_i)}{(r_i + p_i - 2r_i p_i)}$$

where r_i is the proportion of species i among the total kills at a site and p_i is the proportion of species i in the available prey community. The resulting values range from +1 (maximum preference) to -1 (maximum avoidance) (Jacobs 1974). The mean Jacobs' index value for each prey species across studies was calculated (± 1 SE wherever the mean is shown), and these values were tested for significant preference or avoidance using t -tests against an expected value of 0 as they conformed to the assumptions of normality.

The number of species with relatively small sample sizes (i.e. few studies recording them as prey) means that significant preference and avoidance is less likely because at least five Jacobs' index values are required to obtain a significant result, hence ours is a

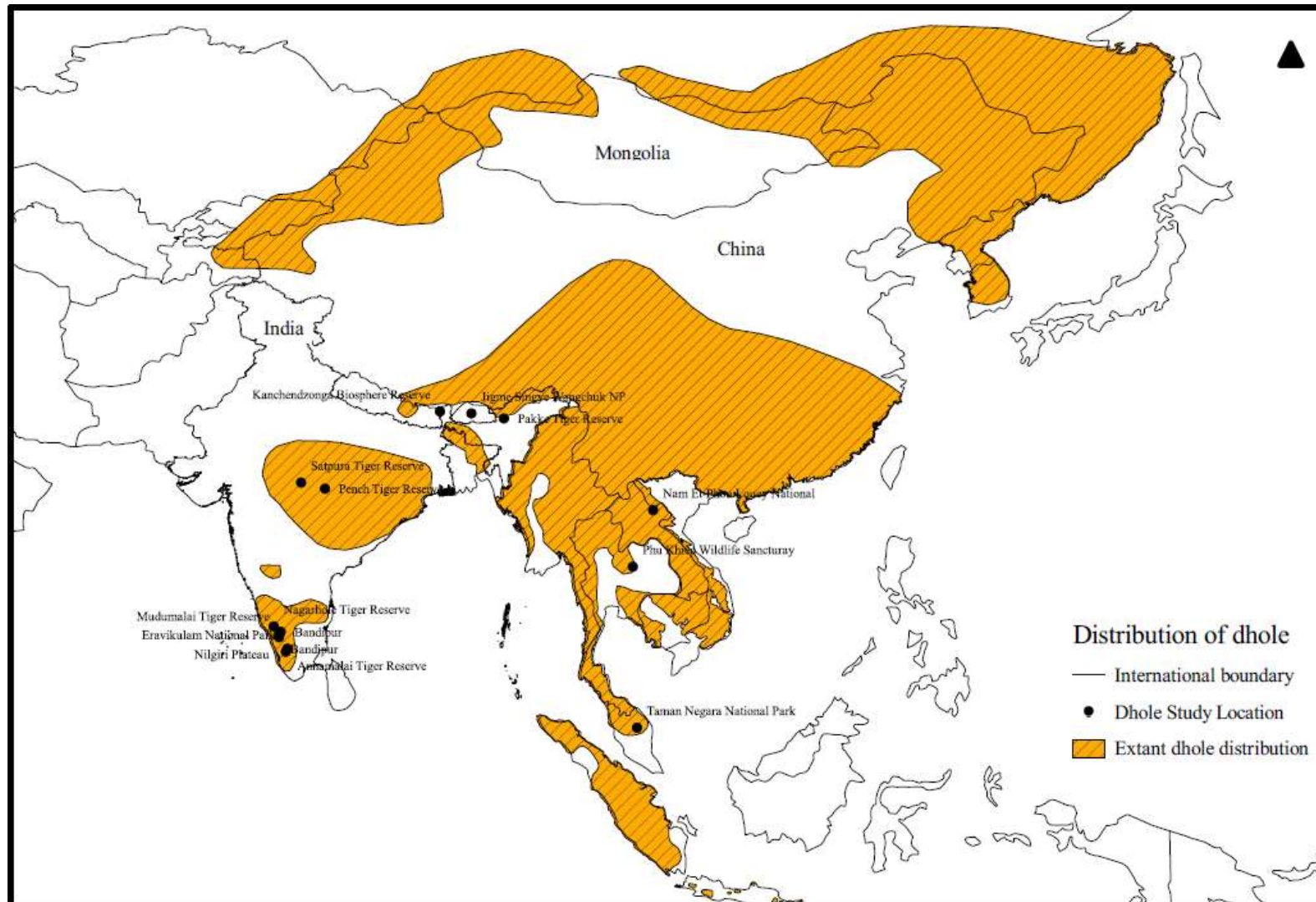


Fig. 1. Locations of the study sites that yielded diet and prey preference information.

Table 1. Details of the studies included in this analysis and their sample sizes. Population estimates from grey literature sources were derived from Distance Sampling. Non-peer reviewed publications are highlighted with an asterix (*).

Dietary data source	Country	Study Areas	Abundance data source	Scats	Kills	Group size
(Wang & MacDonald 2009)	Bhutan	Jigme Singye Wangchuck National Park	Same	138		
(Thinley <i>et al.</i> 2011)	Bhutan	North West Bhutan	Same	70		
(Kumaraguru <i>et al.</i> 2011)	India	Annamalai Tiger Reserve	Same	2074		
(Fox & Johnsingh 1975)	India	Bandipur National Park	(Johnsingh 1992)	138		
(Barnett <i>et al.</i> 1980)	India	Bandipur Tiger Reserve	(Johnsingh 1983)	151		
(Johnsingh 1983)	India	Bandipur Tiger Reserve	Same	509		
(Johnsingh 1992)	India	Bandipur Tiger Reserve	(Johnsingh 1992)	506	302	12.5
(Andheria <i>et al.</i> 2007),	India	Bandipur Tiger Reserve	(Jhala <i>et al.</i> 2011) *	181		
(Rice 1986)	India	Eravikulam National Park	Same	40		22.5
(Selvan <i>et al.</i> 2013b)	India	Kalakad Madutharai Tiger Reserve	(Ramesh <i>et al.</i> 2012b)	78		
(Bashir <i>et al.</i> 2014)	India	Kanchendzonga	Same	41		
(Varman & Sukumar 1993)	India	Mudumalai Tiger Reserve	Same	269		
(Venkataraman <i>et al.</i> 1995)	India	Mudumalai Wildlife Sanctuary	Same	605	58	14.5
(Ramesh <i>et al.</i> 2012a)	India	Mudumalai Tiger Reserve	Same	1438		14.5
(Karanth & Sunquist 1995)	India	Nagarhole Tiger Reserve	Same	188	66	6.5
(Cohen <i>et al.</i> 1978)	India	Nilgiri Plateau	Same	150		3
(Selvan <i>et al.</i> 2013b)	India	Pakke Tiger Reserve	(Gopi <i>et al.</i> 2012) *	163		2.5
(Acharya 2007)	India	Pench Tiger Reserve	Same	725	135	7.5
(Majumder <i>et al.</i> 2011)	India	Pench Tiger Reserve	Same	338		3.5
(Edgaonkar 2008)	India	Satpura Tiger Reserve	Same	81		
(Borah <i>et al.</i> 2009)	India	Satpura Tiger Reserve	(Edgaonkar 2008)	66		
(Kamler <i>et al.</i> 2012)	Laos	Nam Et-Phou Louey National Protected Area	(Vongkhamheng 2011)	76		
(Kawanishi & Sunquist 2008)	Malaysia	Taman Negara National Park	(Kawanishi & Sunquist 2004)	40		
(Grassman <i>et al.</i> 2007)	Thailand	Phu Khieo Wildlife Sancturay	(Prasanai <i>et al.</i> 2012)	172	18	6.5.

conservative measure of prey preference. Nonetheless, plots of Jacobs' index with error bars illustrate which species are likely to be significantly preferred or avoided were a larger sample size available, assuming the existing trend continued.

Multiple regression was conducted on non-correlated, transformed variables to determine which factors influenced the prey preferences of the dhole. The variables used were prey relative abundance at a site, prey body mass, herd size, and preferred habitat type (Table 2). Significant relationships were plotted using linear regression. Linear regression was also used for testing the relationship between prey relative abundance with Jacobs' index value and the proportion of kills at a site. Model selection was based on Akaike's information criterion in a maximum likelihood framework (Akaike *et al.* 1973, Akaike 1974).

We used $\frac{3}{4}$ of adult female body mass to account for juveniles and subadult prey killed following earlier work (Jooste *et al.* 2013). Body masses of prey were taken from our previously published work to allow direct comparisons (Hayward *et al.* 2012, Lyngdoh *et al.* 2014), while that of dholes is taken as $\frac{3}{4}$ of adult female body mass (13kg) to account for subadults participating in hunting (Sillero-Zubiri 2009). We used herd size as an indicator of the ability of prey to detect predators and *vice versa* (Hamilton 1971, Fitzgibbon 1993). This was a categorical variable, with 1 relating to solitary individuals, 2 to species that exist in pairs, 3 to small family grouping species, 4 to small herds (10–19) and 5 to large herds (≥ 20 ; Table 2) following previous work (Lyngdoh *et al.* 2014, Hayward *et al.* 2012, Funston *et al.* 2001).

Habitat type may influence predation rates as the density of vegetation can affect the detectability of both predator and prey (Hayward & Kerley 2005). Animals inhabiting dense vegetation generally adopt a solitary, hider strategy to evade detection, whereas prey on open grasslands are detected by sight rather than sound and often exist in large herds (Geist 1974,

Table 2. Preference status, mean Jacobs's index value of each dhole prey species, number of studies recording it as potential prey (n_p) and actual prey (n_k), mean percentage abundance and kills of each prey species, body mass (three-fourths adult female), and categories of herd size and main habitat based on Nowak (Nowak 1999) and references in (Hayward et al. 2006a).

Species	n_p	n_k	Jacobs' index (D)	SE	t	df	P	Abundance	SE	Kills (%)	SE	Body mass	Herd size	Habitat	
Cattle <i>Bos taurus</i>	3	3	-0.66	0.11				0.40	0.17	0.11	0.03	235	3	1.5	
Deer, chital <i>Axis axis</i> *	16	16	0.14	0.11	1.27	15	0.221	0.46	0.05	0.52	0.04	30	4	1.5	
Deer, mouse <i>Moschiola indica</i> *	3	2	0.31	0.66				0.02	0.02	0.03	0.26	2.5	1	3	
Deer, muntjac <i>Muntiacus muntjak</i>	14	12	-0.01	0.16	-0.06	13	0.951	0.09	0.03	0.13	0.05	14	1	3	
Deer, sambar <i>Rusa unicolor</i>	+	23	22	0.36	0.11	3.48	22	0.002	0.12	0.02	0.21	0.04	200	3.5	2
Elephant <i>Elephas maximus</i>	-	4	0	-1	0	na		0.04	0.01	0	0	2720	3	3	
Gaur <i>Bos gaurus</i>	-	15	8	-0.78	0.07	-10.58	14	<0.001	0.06	0.02	0.02	0.01	650	3	3
Goral <i>Naemorhedus goral</i>		3	3	0.15	0.02			0.17	0.06	0.22	0.07	22	3	2	
Hare <i>Lepus nigricollis</i> *		6	6	0.41	0.21	1.95	5	0.108	0.06	0.02	0.13	0.04	4	1	1
Monkey, langur <i>Semnopithecus entellus</i> *	-	13	8	-0.81	0.14	-5.63	12	<0.001	0.30	0.05	0.02	0.01	5	5	2
Monkey, macaque <i>Macaca spp.</i>		2	1	-0.18	0.82			0.01	0.01	0.04	0.04	9	5	2	
Nilgai <i>Boselaphus tragocamelus</i>		4	3	-0.06	0.38			0.01	0.01	0.02	0.01	169	4	2	
Peafowl <i>Pavo cristatus</i> *		2	0	-1	0			0.10	0	0	0	5	2	2	
Porcupine <i>Hystrix indica</i> *		3	1	-0.95	0.05			0.05	0.00	0.01	0.01	11	1	2	
Serow <i>Capricornis thar</i>		5	4	-0.10	0.27	-0.38	4	0.723	0.18	0.10	0.19	0.09	89	3	1
Squirrels <i>Sciurus spp.</i> *		2	1	-0.05	0.95			0.03	0.03	0.03	0.03	1	1	3	
Tahr <i>Nilgiritragus hylocrius</i>		3	3	-0.57	0.28			0.41	0.17	0.14	0.09	80	4	2	
Wild boar <i>Sus scrofa</i>	-	18	17	-0.30	0.14	-2.12	17	0.049	0.14	0.04	0.08	0.03	47	3	2.5

* small species with densities obtained via Distance Sampling.

Leuthold 1977). As dholes are group hunters reliant upon chasing down their prey (Fox & Johnsingh 1975), we would expect them to predominately hunt prey inhabiting more open habitat types to enable more effective communication and coordinated movement during hunts. A categorical variable of habitat was used with 1 relating to species living in open environments, 2 to those in woodlands and 3 to those inhabiting dense forests (Table 2).

We identified the accessible prey weight range following the methods of Clements *et al.* (Clements *et al.* 2014) and used for snow leopards *Panthera uncia* (Lyngdoh *et al.* 2014). This encompasses the preferred weight range of earlier studies on prey preferences. In summary, prey body mass were ranked and these prey mass-ranks were plotted against corresponding cumulative Jacobs' index +1 values and a segmented model was fitted to these plots. This approach requires the number of break-points in the model to be stipulated before the model is run. The optimum number of break-points (where more than one existed) was therefore selected using AIC in a maximum likelihood framework.

Finally, we used linear regression to test whether there was a relationship between the mean dhole pack size at a site (Table 1) and the mass of the most preferred prey killed, the mass of the most frequently killed prey and the weighted mean mass of prey killed (calculated by summing the products of the body mass of each prey killed and the proportion it was killed).

All analyses and calculations were conducted in *R* (R Core Development Team 2008, Barton 2013). Means are presented with standard errors throughout.

Results

Prey consumption across dhole distribution

We located 24 studies from 16 sites in five of the dholes' 16 range states from all known subspecies (Table 1; Fig. 1). These studies reported on 8237 scats and 579 kills (8816 records) attributed to dholes (scientific names are presented in Table 1).

Sambar (23 sites), wild pig (18), chital (16), gaur (15) and muntjac (14) are the prey species most commonly found in sympatry with dholes (Table 2). Chital, hare, (6), tahr (3), goral (3) and cattle (3) are invariably killed by dholes if they are present at a site (Table 2). Chital (0.46 ± 0.05), tahr (0.41 ± 0.17), cattle (0.40 ± 0.17) and langur monkeys (0.30 ± 0.05) are the most relatively abundant species from the study sites that they occurred, while chital (0.52 ± 0.04), goral (0.22 ± 0.07) and sambar (0.21 ± 0.04) comprise the highest proportion of kills where they occur (Table 2).

Sambar, chital and wild pig contribute almost two-thirds (64%) of the biomass of 35 prey species consumed by dholes, with sambar alone contributing 38% (Fig. 2a). Large wild prey occurs in the diet of the dhole significantly more frequently than smaller wild prey and domestic livestock ($F_{3, 66} = 70.81, p < 0.001$; Fig. 3).

Analysis of data from 579 kills revealed dholes preyed heavily on chital (64.77 %) followed by sambar (32.02 %) with nilgai, hog deer, barking deer, hares and cattle being less commonly taken. There was no distinct preference for juveniles or adults (1:1) in terms of age class of prey killed by dhole. Males were killed marginally more frequently than females (1.2:1).

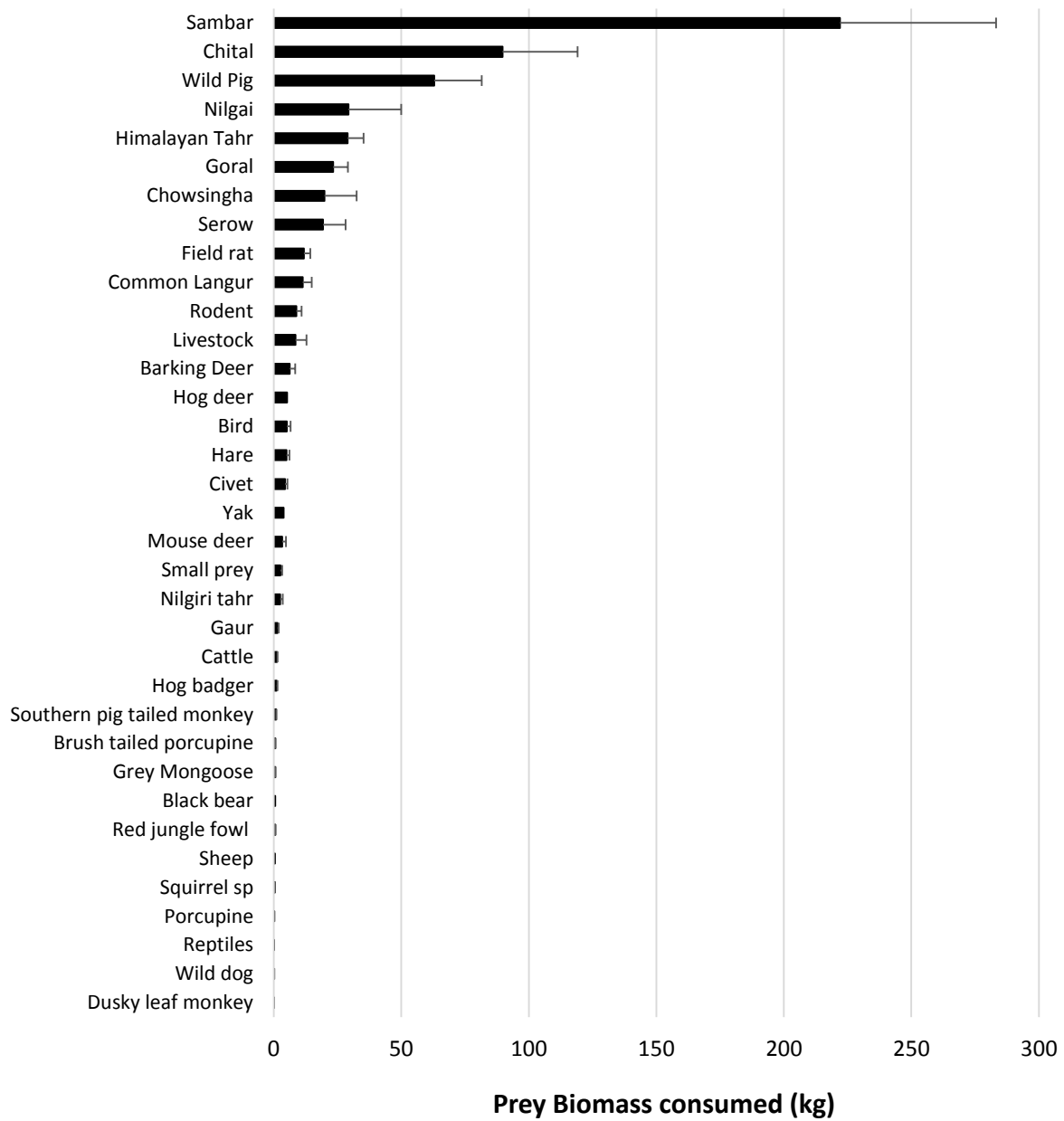


Fig. 2. The contribution of each species to the dietary biomass of dholes (mean \pm 1 S.E.).

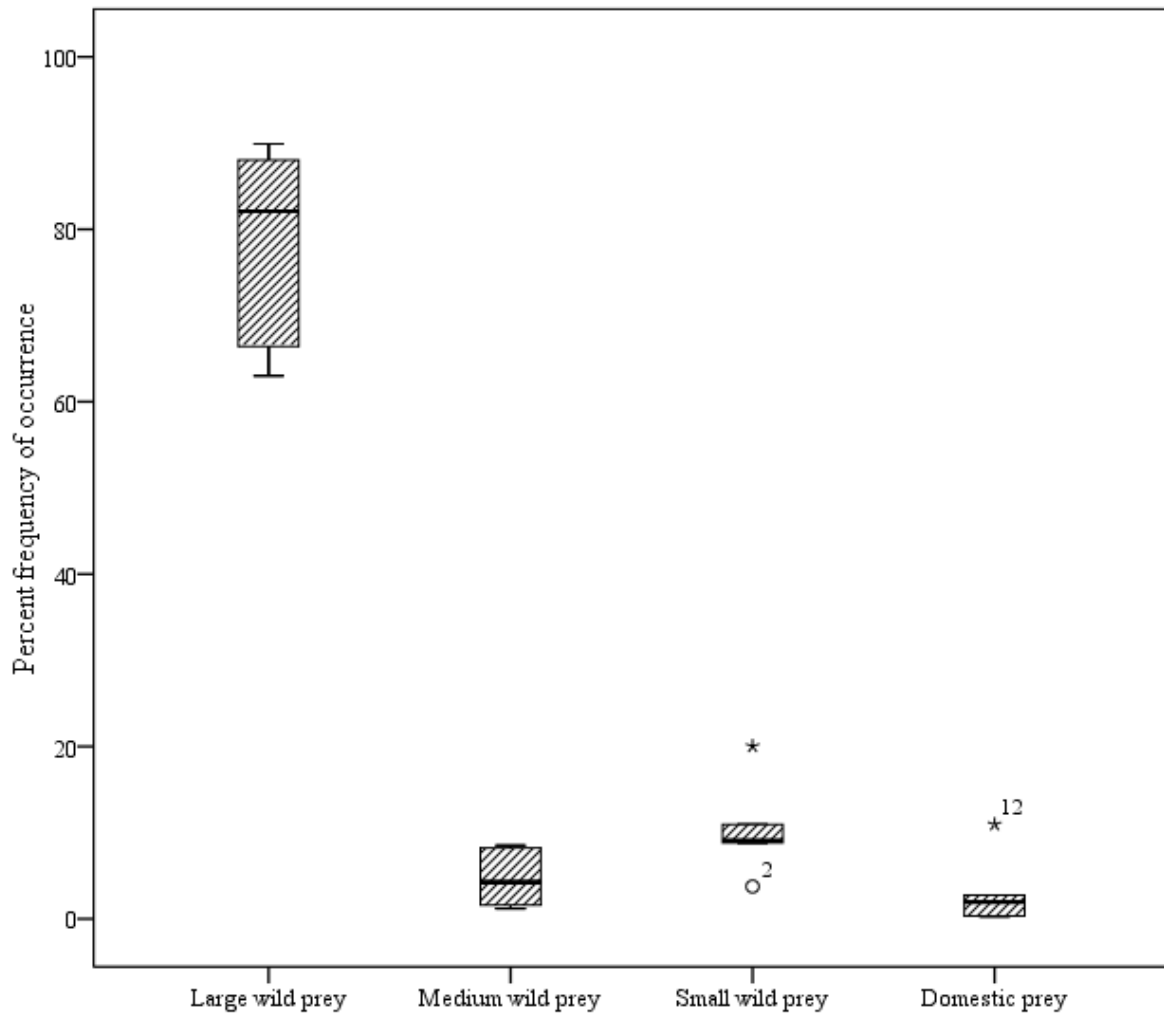


Fig. 3. Box plot of percentage frequency occurrence of prey categories in the diet of dholes.

Prey preference

Sambar are the only prey species significantly preferred by dholes ($D = 0.36 \pm 0.11$), however hares have a higher Jacobs' index value (0.41 ± 0.21) but are not preferred due to their high standard error (Table 2; Fig. 4). Wild pig ($D = -0.30 \pm 0.14$), gaur (-0.78 ± 0.07) and langur monkey (-0.81 ± 0.14) are significantly avoided, while Asian elephant and peafowl are never killed (Table 2; Fig. 4). A larger sample size is likely to see tahr, cattle and porcupine significantly avoided also.

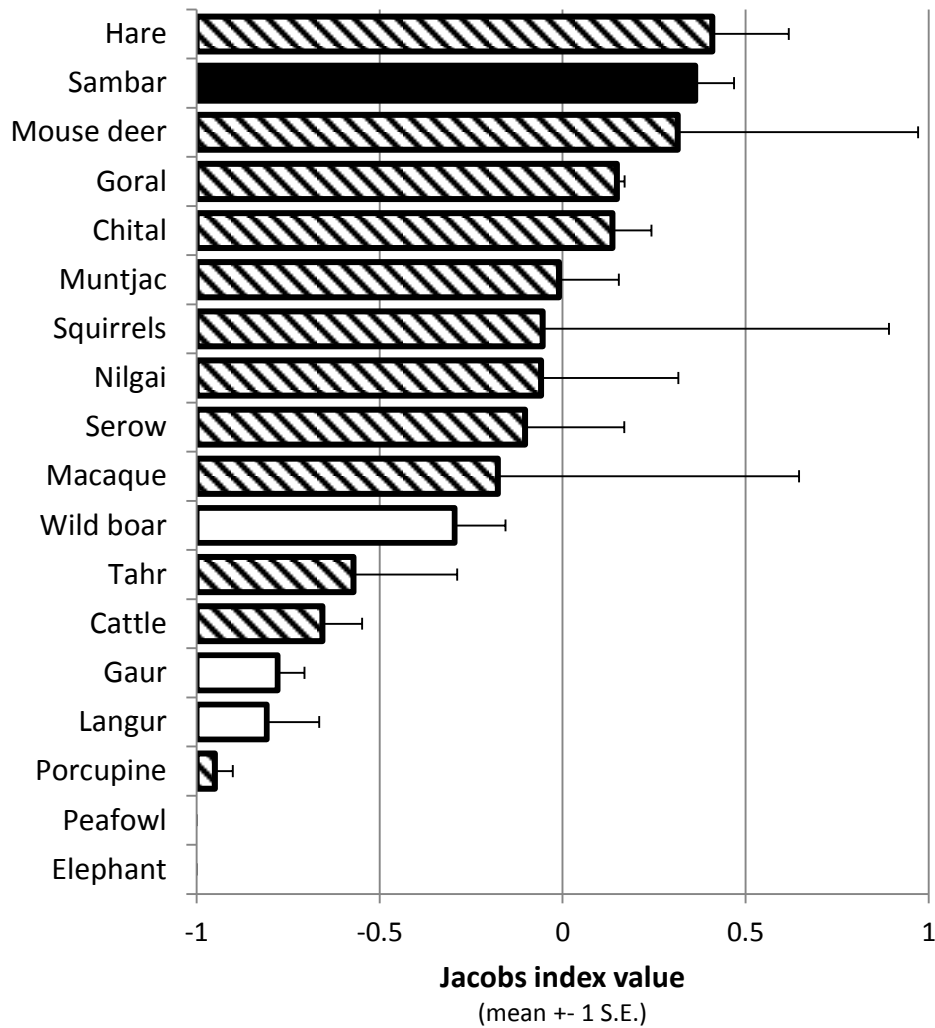


Fig. 4. Prey preferences of the dhole determined using Jacobs' index based on calculated from 11 dhole populations at differing prey densities. Black bars represent significantly preferred species (i.e. those killed significantly more frequently than expected based on their abundance), cross-hatched bars indicate species taken in accordance with their relative abundance and unfilled bars show significantly avoided species (i.e. those taken significantly less frequently than expected based on their abundance).

Dhole most prefer smaller prey, with the exception of sambar, as there is a significant negative relationship between the Jacobs' index values of species killed more than twice and log-transformed prey body mass ($r^2 = 0.47$, $n = 12$, $p < 0.001$; Fig. 5). There are generally

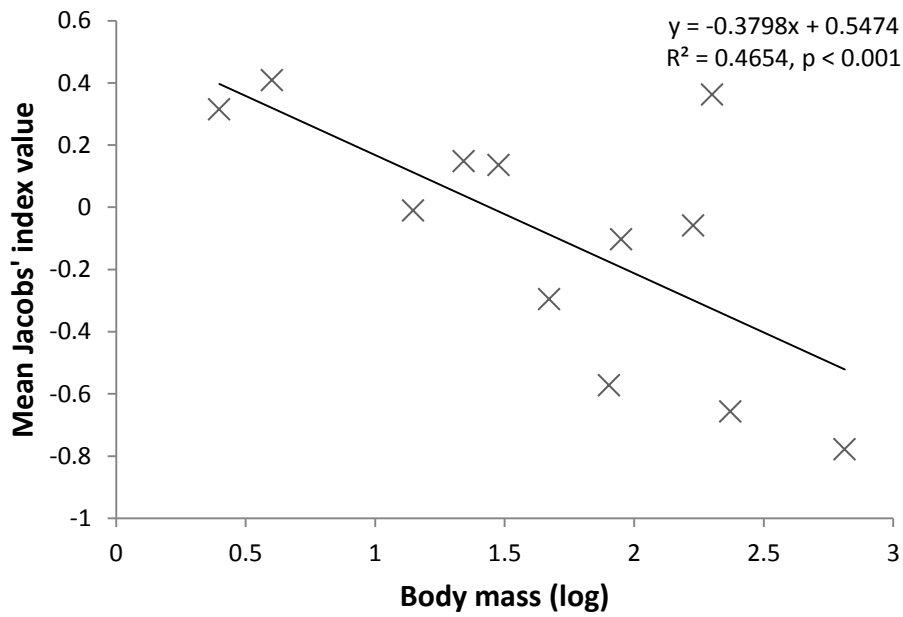
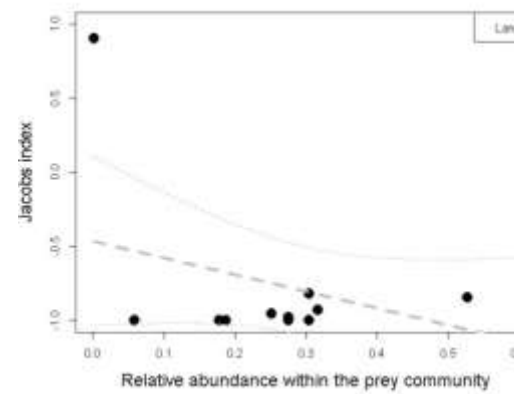
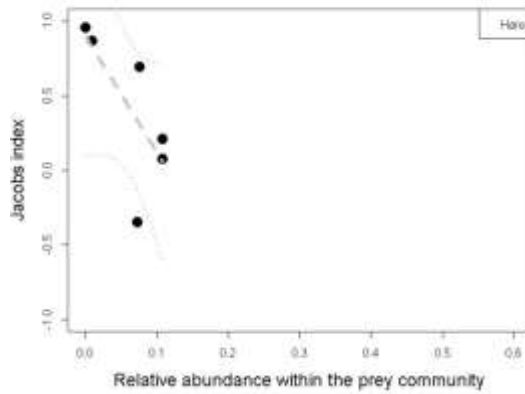
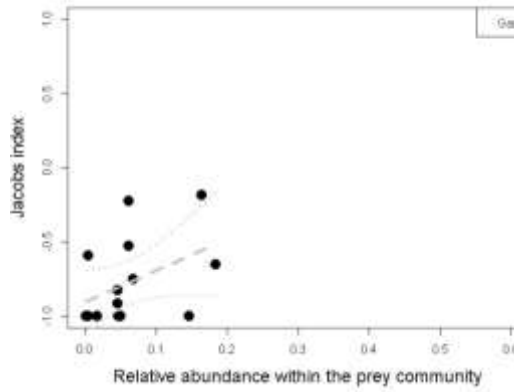
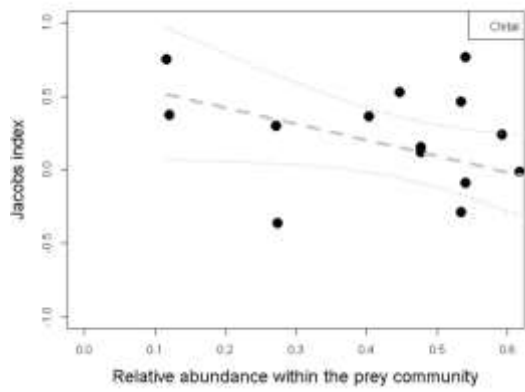
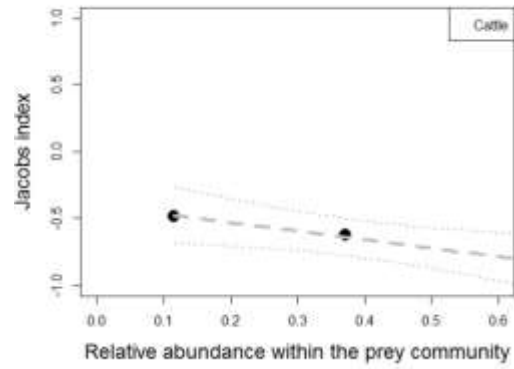
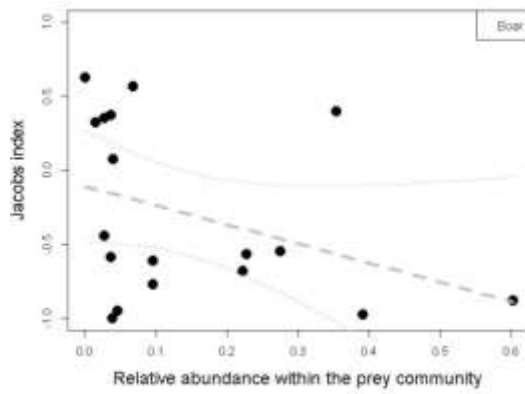


Fig. 5. Relationship between mean Jacobs' index value of prey species with more than two estimates and prey body mass. When two outliers (Indian porcupine and langur monkey) are excluded, this relationship is significant ($r^2 = 0.47$, $n = 12$, $p < 0.001$).

negative relationships exhibited when the Jacobs' index value of each species is plotted against the relative abundance of that species in the community (Fig. 6).



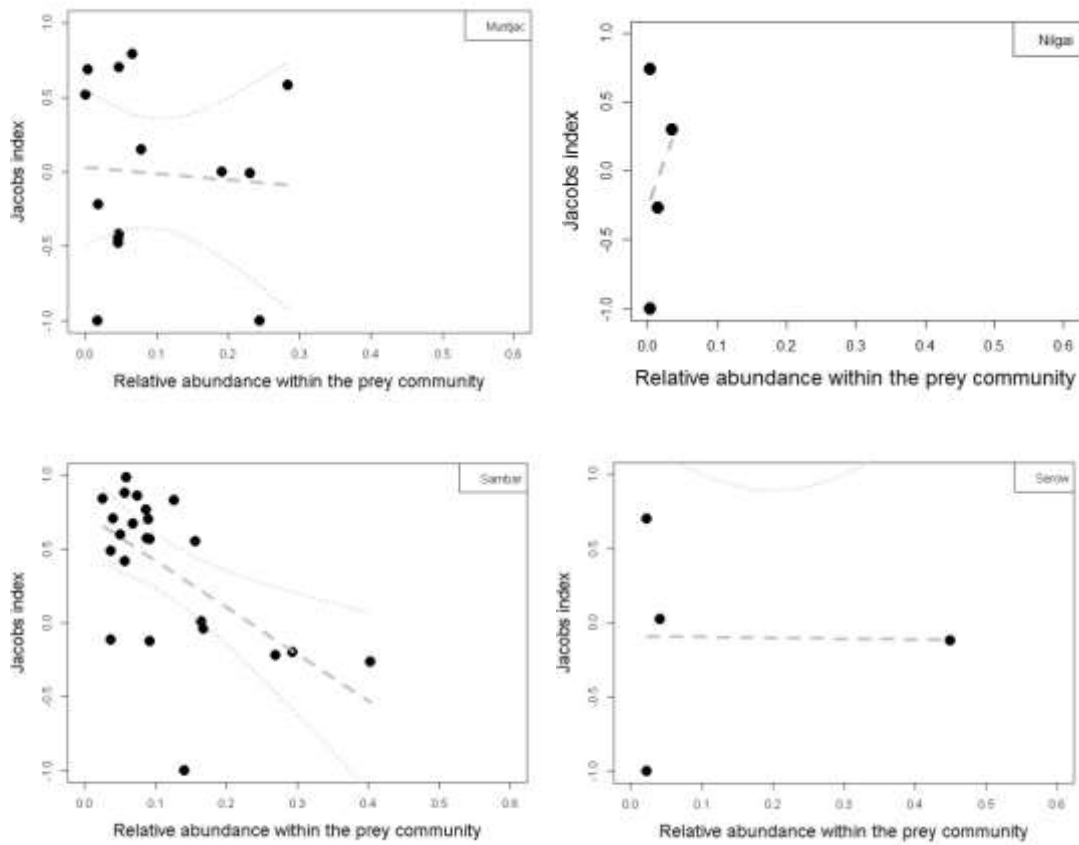


Fig. 6. Relationship between Jacobs' index value for each species at individual sites compared to their relative abundance within the prey community at that site.

Table 3. Generalised linear model results comparing the effect of prey relative abundance, body mass, habitat and herd size against their Jacobs' index values.

Abundance	Body mass	Habitat	Herd size	df	log Likelihood	AICc	ΔAIC_c	Akaike's weight
				2	-8.786	22.7	0	0.383
	-0.0009			3	-7.965	24.3	1.67	0.166
-0.7607				3	-8.342	25.1	2.42	0.114
			-0.0863	3	-8.360	25.1	2.46	0.112
		-0.0987		3	-8.649	25.7	3.03	0.084
-0.8974	-0.0010			4	-7.268	27.0	4.32	0.044
	-0.0008		-0.0651	4	-7.707	27.9	5.2	0.029
-1.09		-0.1961		4	-7.839	28.1	5.46	0.025
	-0.0009	-0.0371		4	-7.945	28.3	5.67	0.022
		-0.1412	-0.1012	4	-8.072	28.6	5.92	0.02

Body mass (kg)	2.5	4	7	9	10	14	17	22	30	36	47	80	89	169	200	235	400	650	2720
Dhole																			
Leopard																			
Tiger																			

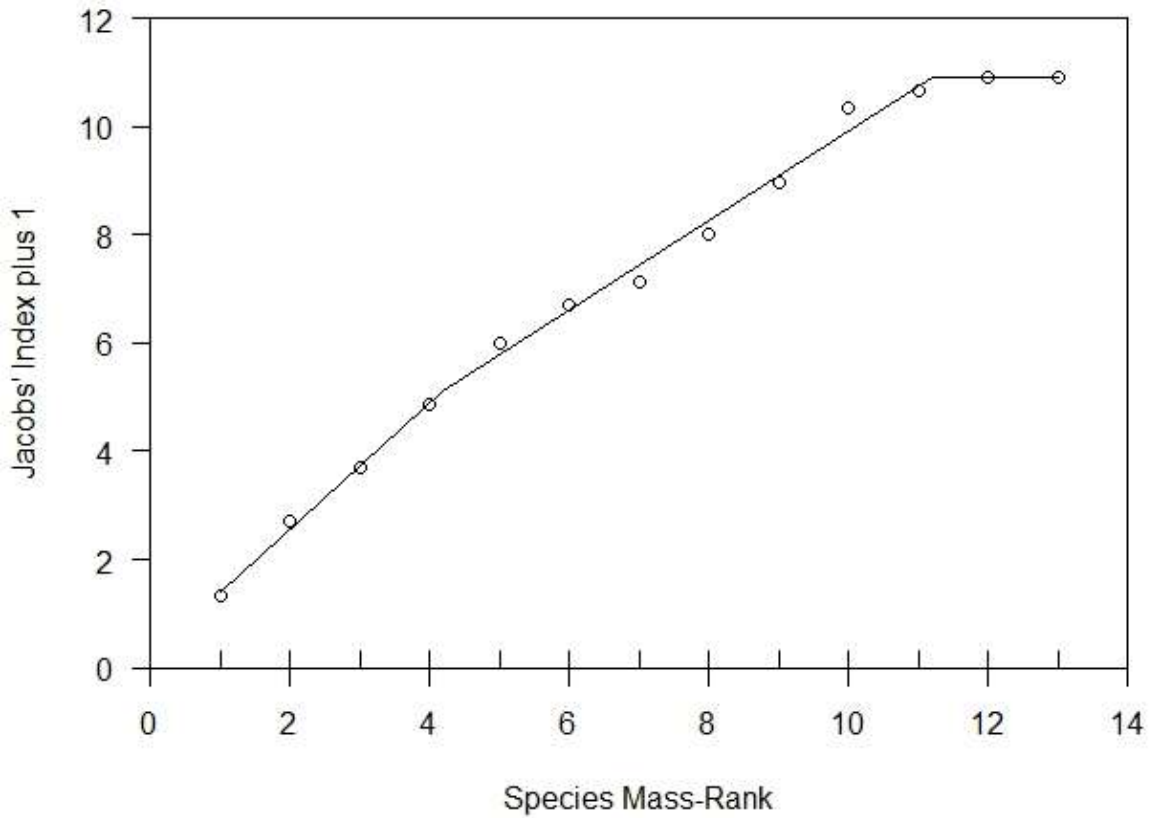


Fig. 7. Segmented model plot for dholes (a) with comparisons to leopards in Asia and tigers based on published data (Hayward et al. 2006a). The dhole model with two breakpoints (b) was most supported in maximum likelihood terms based on Akaike's Information Criterion (AIC). The model with two breakpoints had an AIC value of 2.54, while the other models had Δ AIC values of 14.10, 14.90 and 15.82 for 3, 4 and 1 breakpoint respectively. For leopards and tigers, three breakpoints were most supported. The actual body masses of prey these breakpoints relate to is also shown.

A generalised linear model of the drivers of dhole prey preference revealed the null model was most supported ($AIC_c = 22.7$), but the model that included prey body mass also showed strong support ($\Delta AIC_c = 1.7$; Table 3). Nonetheless, there was no clearly dominant

explanatory variable with body mass (Akaike's weight $w = 0.26$), prey relative abundance ($w = 0.20$), prey herd size ($w = 0.18$) and prey habitat use ($w = 0.16$) all showing low influence.

The mean mass of significantly preferred prey (sambar) is 200 kg. With adult female body mass of dholes being 13 kg, this equates to a predator-to-prey ratio of 1:15. When pack size is considered (2.5-22.5 adults; Table 1), this ratio comes down to 1:0.7-6.2. The segmented model with most support (AIC = 2.53) had two breakpoints and there was no support for any other number of breakpoints ($\Delta\text{AIC} > 14$ for 1, 3 and 4 breakpoints; Fig. 7). The accessible prey weight range of dholes is 30 – 235 kg (Fig. 7). This is larger than the accessible weight ranges of tigers and leopards, although the accessible weight range of tigers extends down to smaller prey (Fig. 7). The preferred weight range, based on a visual interpretation of a less smoothed plot of body mass against Jacobs' index values, was approximately 130 – 190 kg.

Pack size and habitat influences on prey

There was no relationship between dhole pack size and the body mass of the most preferred prey species ($r^2 = 0.074$, $n = 13$, $p = 0.685$; Fig. 8a) or the body mass of the most frequently killed prey species ($r^2 = 0.089$, $n = 13$, $p = 0.169$; Fig. 8b). There was a significant relationship between dhole pack size and the weighted mean mass of prey taken ($r^2 = 0.369$, $n = 13$, $p = 0.016$), however this is heavily influenced by one site (Eravikulam; Fig. 8c).

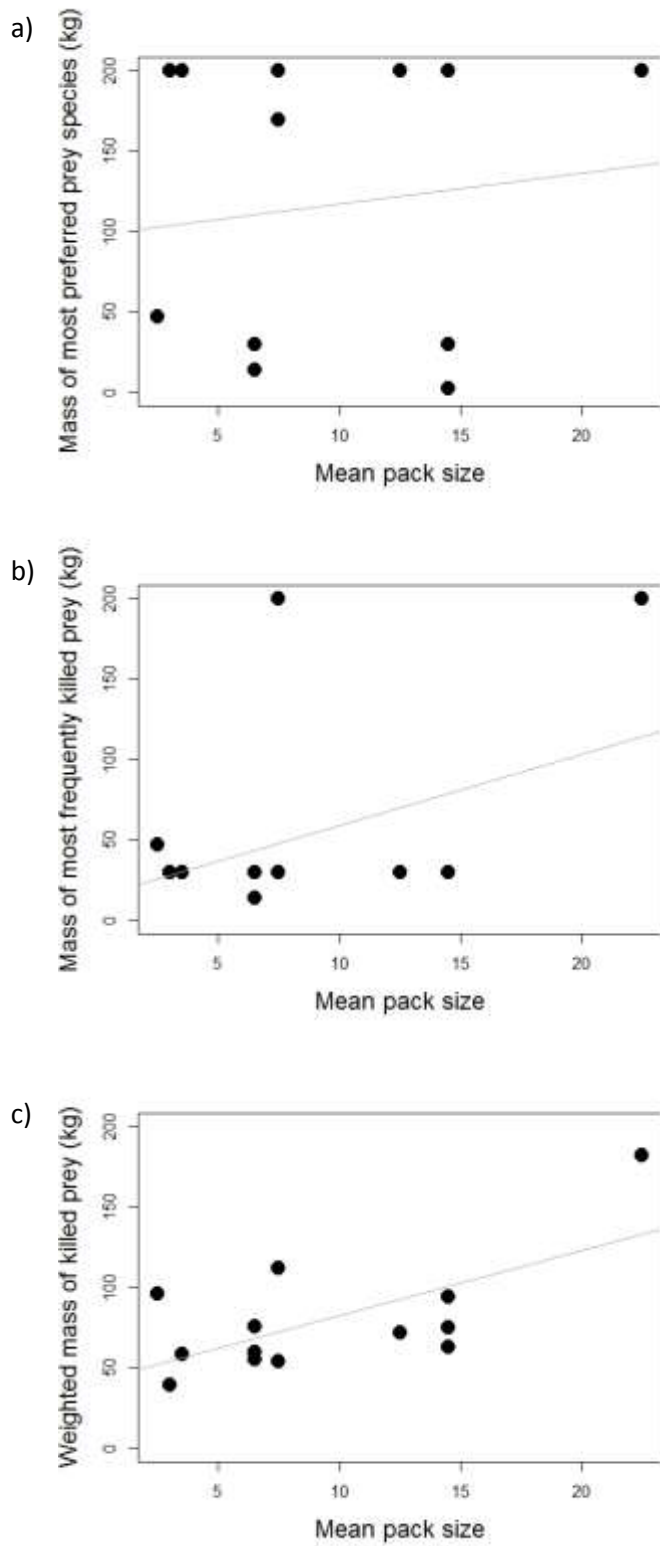


Fig. 8. Relationships between mean dhole pack size and a) body mass of most preferred prey; b) mass of most frequently killed prey; and c) the weighted mean of prey killed by dholes.

Discussion

Hunting in groups affords predators an opportunity to capture prey well beyond the safe size for solitary predators, even if it does not explain the evolution of group living (Packer *et al.* 1990). Dholes hunt in packs of 2.5 – 22.5 individuals and the ratio of predator to prey is 1:15 for individuals, but 1:0.7 – 6.2 for groups of this size. Other group hunters exhibit similar predator to prey ratios (lions *Panthera leo* 1:3.6, African wild dogs *Lycaon pictus* 1:1.4-7.7) in contrast to solitary hunters that prefer prey of equal or slightly smaller size (Hayward 2009). This prey preference is not driven by pack size (Fig. 8a) as was hypothesised to occur in African wild dogs (Hayward *et al.* 2006b), although increasing pack size does allow dholes to prey more heavily on larger prey (Fig. 8c) and pack size may increase hunting success as it does with African wild dogs (Creel & Dugatkin 2001).

This study also highlights the degree of competition that occurs in Asia's large predator guild. Where Africa's predators have clearly partitioned dietary niche among the prey community (Hayward & Kerley 2008), there is a high degree of preferential predatory overlap in Asia's large predators (Fig. 7). Sambar deer are the preferred prey of both tigers (alongside wild boar) and dholes, and are highly preferred by leopards in Asia (Hayward *et al.* 2012, Hayward *et al.* 2006a). Thus, sambar are clearly fundamental prey resources to the large predator guild in Asia and their conservation is crucial for that of Asia's large predator guild. Yet the extreme overlap in accessible prey (Fig. 7) illustrates just how little dietary niche differentiation has evolved in Asia. Jacob's index values of preferred prey between dhole, tiger and leopard show similar patterns (Fig. 7).

Our study contradicts an earlier (Selvan *et al.* 2013a) that concluded that dholes prefer wild pigs and other medium-sized prey. The earlier study was based on a sample size 59% of this present study (5265 cf 8816), from nine publications from three countries, which is much

smaller than used here and so we consider our results more robust. This is not to say wild pigs are not important prey species as they are clearly killed frequently by dholes (Selvan et al. 2013a and our results), but rather that they are killed less frequently than expected based on their relative abundance within the prey community. Sambar and chital are the two main species that are crucial for the survival of the dhole, with the natural abundance of wild pigs making them a key prey resource also. Though an optimum weight range of 40 – 70 kg was suggested, we believe that that dholes are voracious group hunters with prey weighing between 30 – 235 kg accessible and those weighing between 130 and 190 kg preferred. There are also biological reasons why the earlier results are unlikely given that suids are generally only taken by the largest of felids due to their weaponry and low centre of gravity (Hayward et al. 2012).

The high frequency of hares in the diet of dholes concurs with work on African wild dogs. Although hares are not preferred by either species (Hayward *et al.* 2006b), they are frequently taken, and some populations of African wild dogs persist on such small prey (Woodroffe *et al.* 2007). Under an optimal foraging framework, predation on such sub-optimal species is likely if they can be captured and consumed with little effort or risk.

One of the main threats to the status of dholes is a loss of prey base (Durbin *et al.* 2008). This study identifies the key prey resources necessary for the conservation of dholes, and highlights the high potential for dietary competition for these resources amongst Asia's large predator guild.

The study also highlights dholes primarily rely on wild prey; domestic prey seldom contributes to dhole diet (Selvan et al. 2013a, Gopi et al. 2012, Acharya 2007). However, in exceptional cases the dhole does prey on livestock, this has led to major decline in dhole encounters (Lyngdoh *et al.*, In review). As an apex predator the dhole's ecological role in

Asia is evidently relevant in the context of conservation of sympatric large carnivores like tiger and leopard. Our findings thus point out intricate balances that the ecosystems of Asia have maintained through this carnivore trinity and any future conservation efforts must incorporate the entire guild.

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