




Note

# Diet and Prey Selection of Dholes in Evergreen and Deciduous Forests of Southeast Asia

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**ABSTRACT** Endangered dholes (*Cuon alpinus*) are restricted to small and declining populations in Southeast Asia, and little is known about how their ecology differs within the region. We used DNA-confirmed scats and prey surveys to determine the seasonal diet and prey selection of dholes in 2 different landscapes that dominate Southeast Asia: closed evergreen forests in hilly terrain in northern Laos, and open deciduous forests in relatively flat terrain in eastern Cambodia. On both sites, muntjac (*Muntiacus* spp.; 20–28 kg) was the dominant prey item and was selectively consumed over other ungulates in all seasons. Our findings differ from previous conclusions, based largely on studies from India, that the preferred prey weight range of dholes was either 40–60 kg or 130–190 kg. Other important prey were sambar (*Rusa unicolor*) in Laos, and wild pig (*Sus scrofa*) and banteng (*Bos javanicus*) in Cambodia. Seasonal differences in overall diet occurred in Laos, but not Cambodia, primarily because of an increase in livestock consumption. The mean number of dhole scats in group defecation sites was higher in Cambodia ( $5.9 \pm 0.5$  [SE]) than Laos ( $2.4 \pm 0.2$ ), suggesting pack sizes were larger in Cambodia. Our results suggest that regardless of land cover type, prey diversity, or pack size, the management of muntjac will be important for conserving dhole populations in Southeast Asia. In Laos, we recommend that local villagers remove livestock from the protected area during the hot-dry season to reduce livestock predation by dholes. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

**KEY WORDS** Asiatic wild dog, Cambodia, *Cuon alpinus*, diet, Lao PDR, livestock predation, niche breadth, pack size.

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The dhole (*Cuon alpinus*), or Asiatic wild dog, is classified as Endangered by the International Union for Conservation of Nature because it has disappeared from most of its historical range, and remaining populations are fragmented and still declining (Kamler et al. 2015). The main threats to this species include depletion of their prey base, habitat loss, and persecution due to livestock predation (Kamler et al. 2015). Depletion of their prey base might be the single greatest

factor that contributed to their range collapse in the northern parts of their distribution, and might be the primary factor for the continued decline of dholes in the southern parts of their distribution (Kamler et al. 2015). Thus, identifying the preferred prey of different dhole populations is important because conservation of carnivores often requires management and enhancement of their preferred prey (Karanth et al. 2004, Clements et al. 2014). Additionally, dholes are only 1 of 3 canid species with specialized morphological and behavioral adaptations for an exclusively carnivorous diet (i.e., hypercarnivory; Van Valkenburgh 1991). Behavioral traits associated with hypercarnivory include forming exceptionally large packs (often >10 members) to more efficiently hunt and consume large numbers of prey (Johnsingh 1982). Therefore, maintaining relatively high densities of preferred ungulate prey species might be especially important for conserving a hypercarnivorous canid species.

India contains the largest remaining populations of dholes (Kamler et al. 2015), and there have been numerous studies of dhole diets from this country (Selvan et al. 2013, Hayward et al. 2014). Researchers have attempted to determine the body mass of preferred prey of dholes based largely on previous studies of dhole diets from India (Selvan et al. 2013, Hayward et al. 2014). Selvan et al. (2013) reviewed 9 dietary studies from 8 sites and concluded that body mass of preferred prey of dholes was 40–60 kg. Hayward et al. (2014) reviewed 24 dietary studies from 16 sites and concluded that body mass of preferred prey of dholes was 130–190 kg. Taken together, it appears that dholes prefer medium (30–100 kg) and large-sized (>100 kg) ungulates, at least based on studies predominantly from the open and seasonally dry forest ecosystems of India.

In Southeast Asia, where populations of dholes are smaller and more fragmented than India (Kamler et al. 2015), less is known about their diet and prey selection. In contrast to India, most of Southeast Asia is covered in closed evergreen forests, which might influence hunting strategies and preferred prey of dholes. For example, in the closed evergreen forests in Peninsular Malaysia, chevrotains (*Tragulus* spp.), or mouse deer, weighing 1–6 kg (Francis 2008) comprised 78% of the dhole diet (Kawanishi and Sunquist 2008), although prey selection was not determined. Kawanishi and Sunquist (2008) concluded that dholes in Peninsular Malaysia lived in much smaller packs compared to those in India, and hypothesized that the smaller pack sizes are more energetically advantageous in rainforests where large prey is scarce, thick vegetation favors stalk and ambush hunting techniques over cursorial hunting, and food competition with tigers (*Panthera tigris*) and leopards (*P. pardus*) is high. Some additional studies in Southeast Asia have supported this hypothesis, whereas other studies have not. For example, muntjac (*Muntiacus* spp.), a small (<30 kg) ungulate, was the main prey of dholes in Thailand (Grassman et al. 2005, Khoewsree et al. 2020) and Laos (Kamler et al. 2012a). In contrast, sambar (*Rusa unicolor*) and wild pig (*Sus scrofa*), both large (>40 kg) ungulates, were the main prey of dholes in 2 other studies in Thailand (Slangsingha et al. 2007, Charaspet et al. 2015); however, prey selection was not determined in most of the above studies, so whether dholes

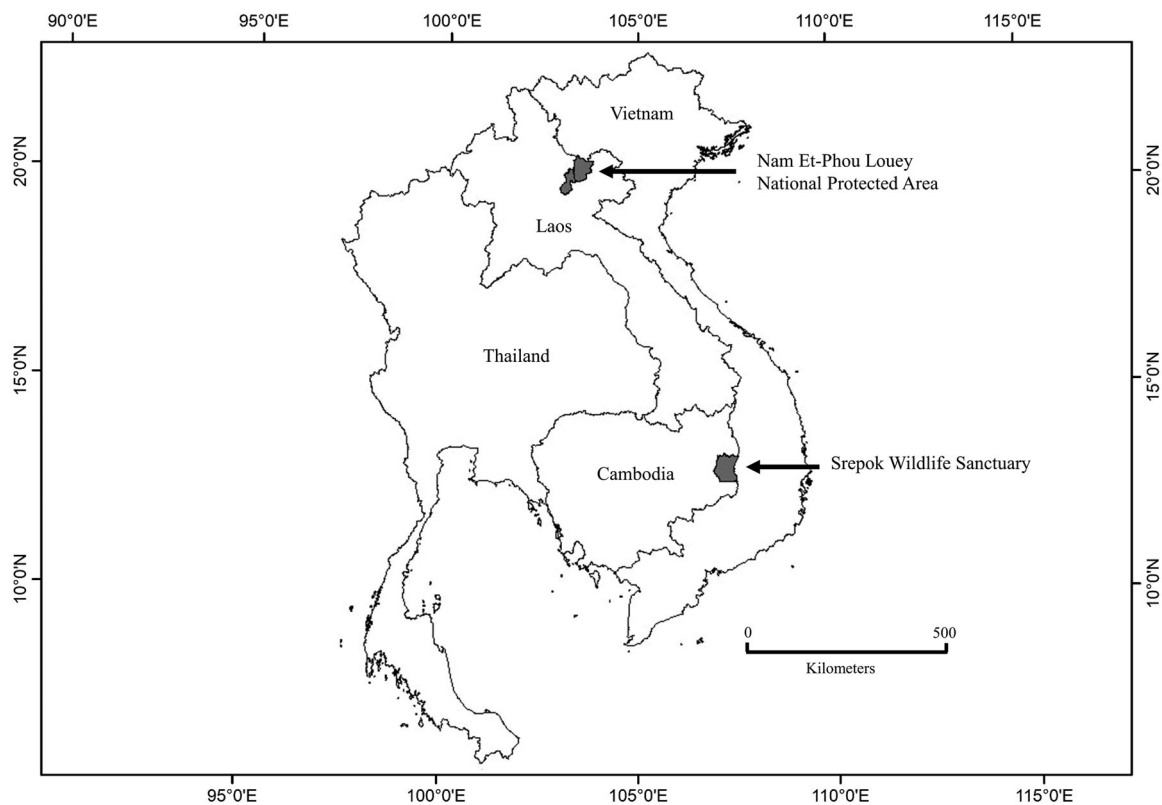
preferentially consume small or large ungulates throughout Southeast Asia is unknown.

Open and seasonally dry deciduous forests, similar to that found in India, cover 15–20% of Southeast Asia (Wohlfart et al. 2014), yet dhole diets within this land cover type have never been studied. If dhole hunting behavior and pack size is affected by land cover type, then prey preferences of dholes should differ between evergreen and deciduous forests in Southeast Asia. Additionally, in India and Bhutan dholes often consume livestock in protected areas (Thinley et al. 2011, Hayward et al. 2014). In contrast, in previous studies conducted in Southeast Asia, dholes did not consume livestock, although livestock grazing was prohibited in the protected areas where those studies occurred. Therefore, more information is needed from protected areas that allow livestock grazing in Southeast Asia to determine if consumption of livestock by dholes is significant in those parks. Increased knowledge regarding livestock predation by dholes is important when devising evidence-based management strategies, especially because persecution due to livestock predation is a major factor contributing to the decline of dholes (Kamler et al. 2015). Furthermore, dholes occupy ecosystems that often exhibit strong seasonal differences in precipitation and temperature, which might affect consumption of prey, including livestock (Thinley et al. 2011), yet the effect of different seasons on the prey selection of dholes has never been studied.

We describe the seasonal diet and prey selection of dholes from 2 protected areas in Southeast Asia in different land cover types: closed evergreen forests in hilly terrain in northern Laos, and open deciduous forests in relatively flat terrain in eastern Cambodia. Livestock grazing was allowed inside the protected area in Laos; thus, we could investigate the extent to which dholes consumed livestock. Based on previous studies, we made 4 predictions: dholes would prefer small (<30 kg) prey in the closed evergreen forests in Laos and larger prey in the open deciduous forests of Cambodia; pack sizes would be smaller in the closed evergreen forests in Laos compared to the open deciduous forests of Cambodia; niche breadth would be higher in Laos than Cambodia given the greater diversity of potential prey in closed evergreen forests; and seasonal differences in diet and prey selection would occur on both sites, owing to strong differences in precipitation and temperature among seasons, which presumably would affect prey movements and availability.

## STUDY AREA

We conducted research on 2 sites in Southeast Asia with substantially different landscapes from 2010 to 2015. The first study site was in the Nam Et-Phou Louey (NEPL) National Protected Area in northern Laos (5,950 km<sup>2</sup>; Fig. 1). The NEPL is dominated by closed evergreen forests covering hilly terrain. The elevation ranges from 400 m to 2,288 m, and about 91% of the area has slopes >12% (Johnson et al. 2006). The vegetation consists of mixed evergreen-deciduous forest up to 1,500 m, transitioning into evergreen forest at 1,500–1,800 m, with interspersions of beech (*Fagus* spp.) and rhododendrons (*Rhododendron* spp.) above 1,800 m (Davidson 1998). Annual rainfall (mainly



**Figure 1.** Locations of Nam Et-Phou Louey National Protected Area, Laos, and Srepok Wildlife Sanctuary, Cambodia, where we studied the diet and prey selection of endangered dholes, 2010–2015.

May to Oct) is 1,400–1,800 mm, and average temperatures range from lows around 5°C (Dec–Feb) to highs around 30°C (May–Jul; Johnson et al. 2006). The NEPL is known for its high biodiversity, especially carnivores and their prey (Johnson et al. 2006, Rasphone et al. 2019). Other large (>15 kg) carnivore species recorded in NEPL during the study period include the tiger, clouded leopard (*Neofelis nebulosa*), Asiatic black bear (*Ursus thibetanus*), and sun bear (*U. malayanus*; Rasphone et al. 2019). Smaller carnivores include 3 felids, 6 viverrids, 3 mustelids, 1 herpestid, and 1 prionodontid (Rasphone et al. 2019). Wild ungulate species recorded in NEPL include gaur (*Bos frontalis*), sambar, Chinese serow (*Capricornis milneedwardsii*), wild pig, and ≥2 species of muntjac (primarily northern red muntjac [*Muntiacus vaginalis*]; Rasphone et al. 2019). The NEPL is officially divided into 2 zones: a protected core zone where all human activity is prohibited, and a managed-use zone where villages and specified livelihoods are permitted following park regulations (Johnson 2012). There are 34 villages in the managed-use zone, with some of these being just inside the designated core zone (Johnson 2012). Additionally, there are unofficial settlements of various sizes used for raising livestock (i.e., sanams) within the managed-use zone and edge of the core zone (Lim 2017). The sanams are used primarily to graze large livestock (domestic water buffalo and cattle), which are the principal source of cash income for villagers, along with some small livestock, including goats (Lim 2017). Therefore, both small and large livestock were potential prey of dholes on this study site.

The second study site was in Srepok Wildlife Sanctuary (SWS; 3,725 km<sup>2</sup>), formerly called Mondulkiri Protection Forest until 2016, located in the Eastern Plains Landscape of Cambodia (Fig. 1). The SWS is dominated (~70%) by open and seasonally dry deciduous dipterocarp forests in relatively flat terrain, interspersed with small patches of mixed deciduous-evergreen forests on hill tops and riparian forests along streams and rivers (Rostro-García et al. 2018). The elevation ranges from 100 m to 400 m. The SWS has a distinct dry season from around November to May, with a pronounced rainy season during the remaining months. Other large (>15 kg) carnivores present in SWS during the study included the leopard and sun bear (Rostro-García et al. 2018). Smaller carnivores present during the study included the golden jackal (*Canis aureus*), jungle cat (*Felis chaus*), leopard cat (*Prionailurus bengalensis*), 4 viverrids, 1 mustelid, and 1 herpestid. The wild ungulate community in SWS is dominated by banteng (*Bos javanicus*), wild pig, and northern red muntjac, with very small numbers of Eld's deer (*Rucervus eldi*), gaur, and sambar (Gray et al. 2013). Overall, the diversity of carnivores and potential prey are lower compared to NEPL. A core zone (~1,700 km<sup>2</sup>), where human access is restricted, is located in the eastern part of SWS. There are no villages within the core zone, and livestock grazing was not permitted. Therefore, we did not consider livestock to be potential prey of dholes on this study site.

## METHODS

We determined the diet of dholes by analysis of scats (i.e., feces) collected from both sites. In Laos, initial analysis of

dhole scats ( $n=76$ ) collected primarily from 2006 to May 2010 in NEPL was published by Kamler et al. (2012a). From June 2010 to March 2012, we collected >100 additional putative dhole scats in NEPL throughout the year to increase the sample size and allow for a seasonal comparison. Research teams collected scats along trails in the core zone of NEPL during camera-trap surveys, and park staff collected scats opportunistically during routine patrolling. In Cambodia, from January 2013 to March 2015, we opportunistically collected scats along dirt roads and trails throughout the core zone of SWS when conducting camera-trap surveys and other research.

For each scat, we recorded the diameter, date, and global positioning system (GPS) location. Packs of dholes hunt, feed, and defecate together (Johnsingh 1982, Karanth and Sunquist 1995, Durbin et al. 2004, Thinley et al. 2011). Specifically, while traveling through their territory, the alpha pair often defecate together along their travel path, then beta pack members will defecate in the immediate vicinity (A. J. T. Johnsingh, Wildlife Institute of India, personal communication). Therefore, we recorded the number of scats in each group defecation site as a proxy for pack size. Dholes do not use latrines, and therefore do not re-visit specific sites to deposit new scats; thus, we were confident that the number of scats in a communal defecation site were a reliable estimate of pack size. We compared the mean number of scats per group defecation site between sites using an independent samples  $t$ -test (Krebs 1989). We sent approximately 10 g of each scat from both sites to the Sackler Institute for Comparative Genomics, American Museum of Natural History (New York, NY, USA) for species identification based on mitochondrial DNA analysis as described by Caragiulo et al. (2014). In Laos, we sent samples of all putative dhole scats for DNA analysis. In Cambodia, where we often found fresh dhole scats in groups of >4 scats, we sent samples of 1–3 scats/defecation site to confirm the species was dhole. We washed and dried remaining parts of the scats in a laboratory. For each scat, we separated hairs, claws, hooves, and bones from different prey species, and visually estimated the percentage of each prey species. We excluded prey items that were considered trace (i.e., 1–2% of scat) from analysis to minimize bias (Kamler et al. 2007). We identified hair samples from each scat to species by examining the structures of the medullas, which became visible under the microscope after soaking hairs in xylene for >24 hours (Rostro-García et al. 2018). We compared medulla structures to those in a reference collection of hairs from known species. Our data collection did not involve direct handling of study animals; therefore, our research was exempt from review by the University of Oxford, Biomedical Sciences, Animal Welfare and Ethical Review Body (AWERB).

We quantified results from scat analysis in terms of the percent biomass consumed because it is ecologically the most relevant parameter (Klare et al. 2011). Following the recommendations of Klare et al. (2011), we also calculated percent volume, and the frequency of occurrence (i.e., percentage of scats containing a particular food item) to

make our results comparable to previous studies. To calculate the percent biomass of consumed prey, we used the linear regression model ( $Y_i = 0.439 + 0.008X_i$ ) developed by Weaver (1993) for gray wolves (*Canis lupus*). In the model,  $X$  is the live weight of prey killed by wolves, whereas  $Y$  is the mass of prey consumed per collected scat ( $i$ ). Although Weaver's equation was applicable to prey sizes down to 1 kg, additional research showed the equation was applicable to prey as small as rats (Jethva and Jhala 2004). Therefore, we used Weaver's equation for all prey sizes in our study (i.e., including rodents that weighed ~0.5 kg). To determine the live weight of ungulates killed by dholes, we used values given by Karanth and Sunquist (1995) who determined the mean live weight ( $X$ ) of several ungulate species killed by dholes, based on their inspection of dhole kills in India. The mean live weights of individuals killed by dholes were estimated to be 75 kg for gaur, 62 kg for sambar, and 31 kg for wild pig (Karanth and Sunquist 1995), indicating dholes tended to kill younger individuals of these species. The mean live weight of banteng and domestic cattle killed by dholes was not estimated by Karanth and Sunquist (1995), so we used the mean live weight of gaur (75 kg) because these species are similar in size to gaur. For Chinese serow and Asiatic black bears, we used a value of 40% of the weight of adult females provided by Francis (2008), assuming that dholes killed younger rather than adult individuals. We used a value of 40% based on results in India (Karanth and Sunquist 1995), in which the mean weight of individual sambar and wild pigs killed by dholes were 38% and 41%, respectively, of the weights of adult females. Similarly, for domestic goats we used a value of 40% of the adult weight provided by Kamler et al. (2012b). For smaller (<12 kg) species, we assumed that dholes killed mostly adults, and therefore we used weights of adults given by Francis (2008). Because Francis (2008) did not list a weight for the brush-tailed porcupine (*Atherurus macrourus*) and Burmese hare (*Lepus peguensis*), we obtained those weights from Nowak (1999) and Flux and Angermann (1990), respectively. We assumed a live weight of 0.5 kg for all rats and large rodents found in scats because these prey items could not be identified to species given the high diversity of small rodents on our study sites (Francis 2008). We excluded arthropods and an unknown mammal (1 scat from each site) from the biomass calculations because we were unable to accurately estimate biomass consumed for these prey items. Based on the biomass of prey categories consumed, we calculated Levin's measure of niche breadth ( $B$ ; Krebs 1989) on both sites. We used results from a concurrent diet study of leopards in SWS (Rostro-García et al. 2018) to calculate the degree of dietary overlap between dholes and leopards using Horn's index of overlap ( $R_0$ ; Krebs 1989) based on biomass consumed, to determine potential competition for prey species in Cambodia.

To determine prey selection of ungulate species consumed by dholes, we calculated Jacobs' (1974) electivity index ( $D$ ) based on biomass consumed versus biomass available. To determine biomass available for each ungulate species, we multiplied adult female weights (i.e., weight of an

**Table 1.** Summary of ungulate densities ( $D$  = animals/km<sup>2</sup>; SE = standard error) estimated in Nam Et-Phou Louey (NEPL) National Protected Area, Laos, using a grid-based occupancy survey in 2008 (Vongkhamheng et al. 2013), and Srepok Wildlife Sanctuary (SWS), Cambodia, using distance-based line transect sampling in 2014 (Rostro-García et al. 2018).

Species	NEPL, Laos		SWS, Cambodia	
	D	SE	D	SE
Muntjac	1.50	0.11	2.08	0.34
Wild pig	3.19	0.15	6.51	1.95
Sambar	0.36	0.01		
Chinese serow	0.22	0.02		
Gaur	0.02	0.003		
Banteng			2.27	0.53

average-sized individual within the population) by estimates of ungulate densities on both sites. We used ungulate densities that were previously reported for the core zones of NEPL (Vongkhamheng et al. 2013) and SWS (Rostro-García et al. 2018; Table 1). We assumed the estimated ungulate densities on both sites (Table 1) were similar in other years of our study. For the available biomass calculations, we used adult female weights given by Francis (2008) based on the lower weight given for each species. Because  $D$ -values of rare species often are biased, we used only those species that were >5% of biomass consumed or constituted >5% of biomass available (Klare et al. 2010). Consequently, we did not calculate  $D$ -values for gaur or livestock in Laos.

To assess seasonal differences in diet, we divided the year into cool-dry season (1 Nov–15 Feb), hot-dry season (16 Feb–15 May), and rainy season (16 May–31 Oct) to parallel major changes in temperature, precipitation, and vegetation. For both sites, the cool-dry season had the lowest mean daily temperatures and lowest monthly rainfall, the hot-dry season had the highest mean daily temperatures with increasing rainfall, and the rainy season had moderate daily temperatures and the highest rainfall (climate data was

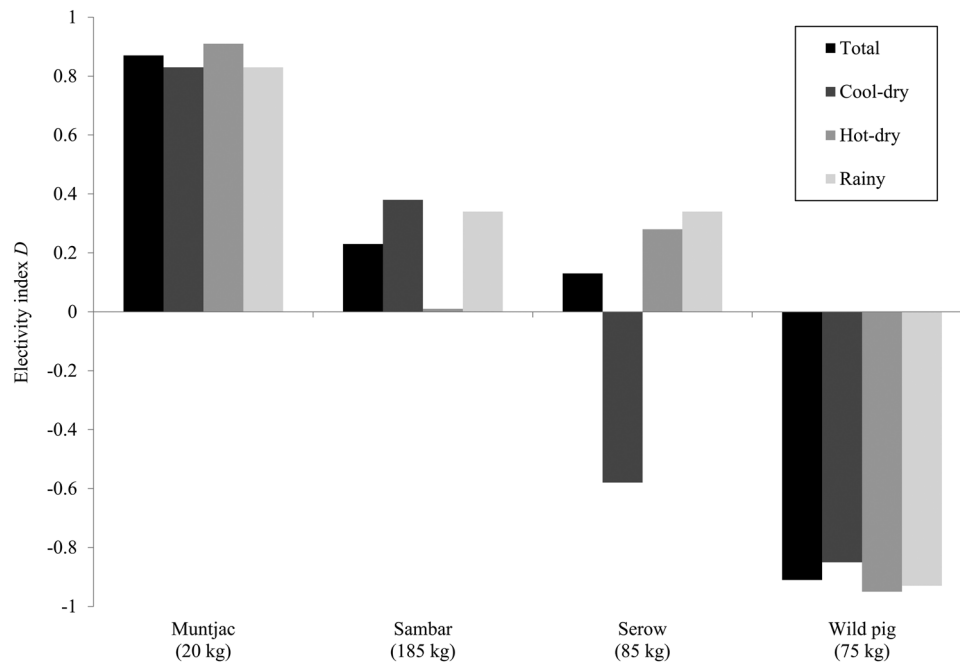
based on Sen Monorom, eastern Cambodia, and Luang Prabang, northern Laos; climate-data.org, accessed 23 Mar 2020). To obtain minimum samples (>30 scats) for each season, we pooled scats across years in each site. In Cambodia, our study site became inaccessible during the rainy season because of high water levels and impassable rivers, so we could not collect and analyze dhole scats for this season. We used chi-square contingency tables to determine if there were differences in diets between seasons. To meet chi-square requirements for sample sizes, we grouped prey categories as muntjac, sambar, wild pig, serow, livestock (cattle and goats), black bear, hog badger (*Arctonyx collaris*), and small (<10 kg) prey for Laos, whereas we used all prey categories for Cambodia. If a significant difference ( $P < 0.05$ ) occurred, then we used Fisher's exact tests to determine which individual prey items significantly differed between seasons. We calculated diet, prey selection, and niche breadth values for each season and total (i.e., combining data from all seasons) on both sites.

## RESULTS

In Laos, 89 scats that we collected from 2010 to 2012 were confirmed by DNA analysis to be from dholes. Together with the 76 DNA-confirmed dhole scats from a previous study (Kamler et al. 2012a), we used 165 dhole scats in our analysis. A majority of scats (70%) contained 1 prey item, whereas remaining scats contained 2 or 3 prey items. Overall, we identified 13 prey species in the scats, including 7 ungulates (5 wild and 2 domestic species). Ungulates comprised 89% of all biomass consumed, followed by carnivores (8%) and rodents (3%; Table 2). Muntjac was the most dominant prey (49% of biomass consumed), followed by sambar (23%), whereas no other species comprised >10% of biomass consumed (Table 2). There was a significant difference in overall diet between the cool-dry and hot-dry seasons in Laos ( $\chi^2 = 18.94$ ,  $P = 0.008$ ) but not between the

**Table 2.** Seasonal diet composition of dholes in Nam Et-Phou Louey National Protected Area, Laos, 2005–2012 ( $n$  = number of scats analyzed), expressed as percentage of ingested biomass (bio), percentage of scat volume (vol), and frequency of occurrence (occ). Dietary niche breadth ( $B$ ) is based on biomass consumed.

Prey category	Cool-dry ( $n = 57$ )			Hot-dry ( $n = 76$ )			Rainy ( $n = 32$ )			Total ( $n = 165$ )		
	Bio	Vol	Occ	Bio	Vol	Occ	Bio	Vol	Occ	Bio	Vol	Occ
Ungulate	83.6	77.9	82.5	89.1	85.9	88.2	97.5	96.7	96.9	88.9	85.2	88.5
Muntjac spp.	41.5	44.4	52.6	54.7	58.4	68.4	48.0	54.0	59.4	48.8	52.7	61.2
Sambar	27.9	20.1	22.8	15.5	11.1	13.2	30.2	22.9	28.1	22.7	16.5	19.4
Wild pig	11.5	11.3	14.0	3.8	3.8	5.3	7.0	7.3	9.4	7.1	7.1	9.1
Chinese serow	1.2	1.1	7.0	7.3	6.9	14.5	9.6	9.5	12.5	5.7	5.4	11.5
Gaur	0.0	0.0	0.0	1.9	1.3	1.3	0.0	0.0	0.0	0.9	0.6	0.6
Domestic cattle	1.5	1.0	3.5	4.3	2.8	6.6	0.2	0.2	3.1	2.5	1.6	4.8
Domestic goat	0.0	0.0	0.0	1.6	1.7	7.9	2.5	2.8	3.1	1.2	1.3	4.2
Carnivore	9.5	11.6	15.8	9.5	10.8	17.1	2.5	3.3	6.3	8.1	9.6	14.5
Asian black bear	2.9	2.5	5.3	4.7	4.1	9.2	0.2	0.2	3.1	3.1	2.8	6.7
Asian palm civet	2.8	4.1	5.3	1.3	2.0	2.6	0.0	0.0	0.0	1.6	2.3	3.0
Hog badger	3.9	5.0	7.0	2.7	3.4	6.6	2.3	3.1	3.1	3.0	3.9	6.1
Leopard cat	0.0	0.0	0.0	0.9	1.3	1.3	0.0	0.0	0.0	0.4	0.6	0.6
Rodent	6.9	10.5	14.0	1.3	2.0	2.6	0.0	0.0	0.0	3.0	4.5	6.1
Brush-tailed porcupine	1.0	1.5	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5	1.2
Small (<1 kg) rodent	5.9	9.1	12.3	1.3	2.0	2.6	0.0	0.0	0.0	2.6	4.0	5.5
Unknown mammal		0.0	0.0		1.3	1.3		0.0	0.0		0.6	0.6
Niche breadth ( $B$ )	3.70			2.98			2.97			3.31		



**Figure 2.** Jacobs' (1974) electivity index ( $D$ ) of ungulates based on percent biomass consumed by dholes in Nam Et-Phou Louey National Protected Area, Laos, 2010–2012. Body mass of each species represents the adult female body mass reported by Francis (2008).

hot-dry and rainy seasons ( $\chi^2 = 8.38$ ,  $P = 0.300$ ) or rainy season and cool-dry seasons ( $\chi^2 = 9.33$ ,  $P = 0.230$ ; Table 2). When comparing individual prey categories between the cool-dry and hot-dry seasons, only livestock (cattle and goats) significantly differed between seasons ( $P = 0.041$ ). The biomass of ungulates consumed by dholes in Laos did not reflect the biomass available because overall dholes showed a strong selection for muntjac ( $D = 0.87$ ) and avoided wild pig ( $D = -0.91$ , Fig. 2). The electivity values were relatively stable across seasons because dholes consistently had a strong selection for muntjac ( $D = 0.83$  to  $0.91$ ) and avoided wild pig ( $D = -0.85$  to  $-0.95$ ; Fig. 2). Niche breadth values were highest in the cool-dry season but were relatively low across seasons and overall (Table 2).

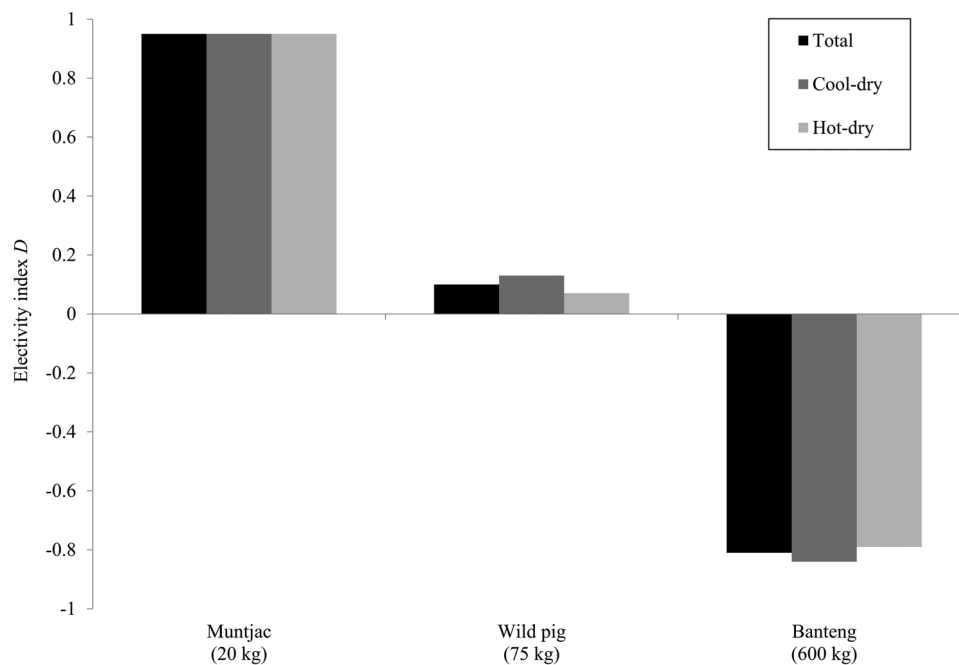
In Cambodia, we used 165 scats, collected from 2013 to 2015, that were confirmed by DNA analysis to be from dholes. A majority of scats (61%) contained 1 prey item, whereas remaining scats contained 2 or 3 prey items. There

were 8 prey species identified in the scats, including 3 ungulates. Ungulates comprised 92% of all biomass consumed, followed by macaques (*Macaca* spp.; 4%), Asian palm civet (*Paradoxurus hermaphroditus*; 3%), and Malayan porcupine (*Hystrix brachyura*; 1%; Table 3). Muntjac was the most dominant prey (45% of biomass consumed), followed by wild pig (28%) and banteng (19%); no other species comprised >10% of biomass consumed (Table 3). The diet did not differ between the cool-dry and hot-dry seasons in Cambodia ( $\chi^2 = 5.36$ ,  $P = 0.616$ ). The biomass of ungulates consumed by dholes did not reflect the biomass available in Cambodia because overall dholes showed a strong selection for muntjac ( $D = 0.95$ ) and avoided banteng ( $D = -0.81$ ; Fig. 3). Electivity values were stable across seasons because dholes consistently had a strong selection for muntjac ( $D = 0.96$  in both seasons) and avoided banteng ( $D = -0.79$  and  $-0.84$ ; Fig. 3). Niche breadth values were similar and relatively low across seasons and overall (Table 3). The

**Table 3.** Seasonal diet composition of dholes in Srepok Wildlife Sanctuary, Cambodia, 2013–2015 ( $n$  = number of scats analyzed), expressed as percentage of ingested biomass (bio), percentage of scat volume (vol), and frequency of occurrence (occ). Dietary niche breadth ( $B$ ) is based on biomass consumed.

Prey category	Cool-dry ( $n = 71$ )			Hot-dry ( $n = 94$ )			Total ( $n = 165$ )		
	Bio	Vol	Occ	Bio	Vol	Occ	Bio	Vol	Occ
Ungulate	92.1	88.0	88.7	92.6	89.3	89.4	92.4	88.7	89.1
Northern red muntjac	46.0	48.7	49.3	44.6	48.5	61.7	45.2	48.6	56.4
Wild pig	29.3	28.5	46.5	27.0	27.0	56.4	28.0	27.6	52.1
Banteng	16.7	10.8	16.9	21.0	13.8	18.1	19.2	12.5	17.6
Asian palm civet	2.9	4.2	4.2	2.5	3.7	4.3	2.7	3.9	4.2
Macaque <sup>a</sup>	5.0	7.0	7.0	3.0	4.3	4.3	3.9	5.5	5.5
Malayan porcupine	0.0	0.0	0.0	1.2	1.6	3.2	0.7	0.9	1.8
Burmese hare	0.0	0.0	0.0	0.7	1.1	1.1	0.4	0.6	0.6
Fresh-water crab (Potamidae)		0.7	1.4		0.0	0.0		0.3	0.6
Niche breadth ( $B$ )	3.04			3.14			3.11		

<sup>a</sup> Long-tailed macaque (*Macaca fascicularis*) or northern pig-tailed macaque (*M. leonina*).



**Figure 3.** Jacobs' (1974) electivity index ( $D$ ) of ungulates based on percent biomass consumed by dholes in Srepok Wildlife Sanctuary, Cambodia, 2013–2015. Body mass of each species represents the adult female body mass reported by Francis (2008).

dietary overlap between dholes and leopards in SWS was relatively high ( $R_0=0.88$ ). The mean ( $\pm$ SD) number of fresh scats per group defecation site was significantly higher ( $P<0.001$ ) in Cambodia ( $5.9 \pm 2.7$ ; range = 1–11,  $n=28$ ) than Laos ( $2.4 \pm 1.1$ ; range = 1–6,  $n=22$ ).

## DISCUSSION

In both Laos and Cambodia, muntjac (20–28 kg) was the dominant prey item and was selectively consumed by dholes over other ungulates in all seasons. These findings differ from previous conclusions, based largely on studies from India, that the preferred prey weight range of dholes was either 40–60 kg or 130–190 kg (Selvan et al. 2013, Hayward et al. 2014). Our results partially supported our first prediction, which stated that dholes would prefer small ungulates in the closed evergreen forests of Laos, similar to that reported in Malaysia (Kawanishi and Sunquist 2008). This prediction also stated that dholes would prefer larger prey in the open deciduous forests of Cambodia, similar to that reported in India, but this part of the prediction was not supported. Instead, on both sites muntjac comprised a similar proportion of the dhole diet, and had similarly high electivity values.

The high consumption and strong selection for muntjac on both sites might have been due to different reasons on each site. In Laos, the closed evergreen forests likely facilitated smaller packs and favored ambush hunting techniques (Kawanishi and Sunquist 2008), which in turn led dholes to consistently select most for muntjac in all seasons. This was corroborated by our data, which indicated pack size of dholes in Laos was significantly smaller than in Cambodia, and similar to small pack sizes of dholes previously reported in Malaysia (1–4 individuals; Kawanishi and Sunquist 2008). The strong selection for muntjac was not

related to a high prey density of this species because the density of wild pigs in Laos was twice as high as muntjac. Wild pigs are relatively aggressive compared to other ungulates, and males have tusks to aid in their defense; thus, wild pigs are more dangerous to hunt and handle for dholes compared to other ungulates (Johnsingh 1992). Additionally, wild pigs live in groups, which may make them more efficient at detecting and avoiding predation (Kamler et al. 2012a). Consequently, wild pigs typically comprise a relatively low proportion of dhole diets across Asia regardless of wild pig densities (Kamler et al. 2012a); thus, it was not surprising that wild pigs consistently had the most negative electivity values across seasons in Laos. Additionally, sambar density was relatively low ( $0.4$  sambar/ $\text{km}^2$ ) in Laos, especially compared to densities of this species at sites occupied by dholes in India ( $3.4$ – $10.0$  sambar/ $\text{km}^2$ ; Karanth and Sunquist 1995, Kumaraguru et al. 2011, Majumder et al. 2012, Ramesh et al. 2012). Although sambar is one of the main preferred prey of dholes in India (Selvan et al. 2013, Hayward et al. 2014), the small pack sizes of dholes in Laos, combined with the low density of sambar, might have prevented dholes from efficiently hunting and consuming large numbers of sambar, the largest cervid in the study site. Chinese serow ( $85$ – $140$  kg; Francis 2008) is smaller than sambar and within the reported weight range of preferred dhole prey (Selvan et al. 2013, Hayward et al. 2014), yet muntjac were consistently selected over serow in all seasons, and serow comprised only 6% of biomass consumed (Table 1). Serow prefer more steep terrain compared to the other ungulates in NEPL (Francis 2008), and had a lower density than muntjac and sambar. Thus, despite the ideal body mass of serow, dholes may not have selectively hunted this species because of its low density and preference for steep terrain, for which the cursorial

hunting strategy of dholes is not well adapted (Kamler et al. 2012a). Our results are consistent with the findings of a previous study of dhole diets in NEPL (Kamler et al. 2012a), indicating the consumption patterns and prey selection of dholes are relatively stable across years. Overall, our findings suggest that the closed evergreen forests of Laos facilitated smaller pack sizes of dholes, which in turn led dholes to select muntjac over other ungulates because of its small body size, solitary behavior, lack of preference for steep terrain, and small defense weaponry compared to the other sympatric ungulates.

Pack size of dholes was significantly larger in Cambodia than in Laos, which supported our second prediction. But dholes still had high consumption and high electivity values for muntjac in Cambodia, which did not support our first prediction that dholes would select for larger ungulates in the open deciduous forests of Cambodia. The ungulate community was less diverse in Cambodia than in Laos; thus, the main potential alternatives to muntjac were wild pig and banteng. In contrast, the open deciduous forests in India are often dominated by 2 large cervids, chital (*Axis axis*) and sambar (Karanth and Sunquist 1995, Kumaraguru et al. 2011, Majumder et al. 2012, Ramesh et al. 2012), which were the only 2 prey species found to be significantly preferred by dholes (Selvan et al. 2013, Hayward et al. 2014). Historically, a large cervid, Eld's deer (95–150 kg; Francis 2008), occurred in the open deciduous forests of eastern Cambodia in large herds, although overhunting by humans has decimated the population and this species is now functionally extinct in the ecosystem (Gray et al. 2013). So perhaps historically, dholes in eastern Cambodia would have most preferred Eld's deer, but now they have shifted to the smaller muntjac in the absence of a large cervid. The strong selection for muntjac in Cambodia was not related to a high prey density of this species because the density of wild pigs was 3 times higher than muntjac, and the density of banteng was similar to muntjac. As in Laos, dholes in Cambodia were unlikely to have a high selection for wild pigs because this species is more dangerous for dholes to hunt and handle. Similarly, banteng is likely too large for dholes to handle and predate efficiently, at least when hunting in packs of about 6 individuals. Nonetheless, wild pig and banteng comprised 28% and 19% of dhole diets, respectively, in Cambodia, supporting the previous finding that larger packs of dholes take larger prey (Hayward et al. 2014). The relatively low diversity of ungulate prey also likely explained the relatively high dietary overlap (0.88) between dholes and leopards in Cambodia because both large carnivores had to focus predation on relatively few ungulate species.

Niche breadth values were similar between sites, which did not support our third prediction. We had predicted that the niche breadth of dholes would be higher in Laos owing to the higher diversity of potential prey in Laos (Johnson et al. 2009, Rasphone et al. 2019). Dholes did consume more species in Laos than Cambodia (13 and 8 species, respectively); however, their primary consumption on both sites focused on muntjac and a few other ungulate species, leading to similarly low niche breadth values on both sites. This result is probably due to the hypercarnivory of dholes, which forces them to consistently

hunt and consume large numbers of ungulates (Kamler et al. 2012), rather than being more of a generalist predator, regardless of the diversity of potential prey. Nonetheless, other carnivores were found in 15% of dholes scats in Laos, with Asiatic black bears, hog badgers, and Asian palm civets being the most frequently consumed carnivores. The relatively high consumption of carnivores by dholes in Laos is somewhat unusual because carnivores are not frequently found in dhole diets, at least in India. In fact, no previous study in Asia reported consumption of bear by dholes (Naing et al. 2019), suggesting consumption of bears in Laos could have been due to scavenging, or predation on cubs. In Thailand, previous studies did report relatively high consumption of smaller carnivores by dholes, including hog badgers (Slangsingha et al. 2007) and  $\geq 3$  species of civets (Charaspet et al. 2015, Khoewsree et al. 2020). This suggests that in the evergreen forests of Southeast Asia, consumption of other carnivores might be relatively high because the smaller pack sizes of dholes, along with low densities of sambar and other large ungulates, likely facilitated predation on smaller species.

Seasonal differences in diet occurred in Laos, which supported our fourth prediction. In Cambodia, there was no seasonal difference in diets, although lack of scats from the rainy season prevented us from comparing dhole diets among all seasons. Surprisingly, our results from Laos showed there was no significant difference in diets between the rainy season and both dry seasons. Instead, the only significant seasonal difference in Laos occurred between the cool-dry and hot-dry seasons. Among the prey categories, consumption of livestock (cattle and goats) contributed most to the seasonal difference in diets, with a significantly increased consumption during the hot-dry season. At our study site in Laos, most villagers (56%) removed their livestock from grazing areas inside the park during the dry season, and instead grazed the cattle in paddy fields outside the park (Lim 2017); however, the majority (60%) of one ethnic group, the Lao Sung, kept their livestock grazing in the park year around (Lim 2017). The Lao Sung were the only 1 of 3 ethnic groups in the park that had a majority of their people (61%) experience livestock predation by dholes from 2007 to 2012 (Lim 2017). Our results suggest that livestock losses by dholes reported by the Lao Sung could be reduced if this ethnic group also removed their livestock from the park, or employed better livestock guarding practices, during the hot-dry season.

Overall, our results suggest that despite the dramatic declines of Eld's deer, sambar, gaur, banteng, and other large ungulates in Southeast Asia (Gray et al. 2013, Timmins et al. 2015, Duckworth et al. 2016), dholes could persist in the region if muntjac populations are maintained in adequate numbers. Future research should determine the minimum numbers of muntjac and other ungulates that are needed to sustain a viable dhole population. This information is especially important in Southeast Asia, where muntjac and other prey species face steep declines because of the snaring crises in the region (Gray et al. 2017), which might result in local prey numbers that are too low to sustain viable dhole populations.



## MANAGEMENT IMPLICATIONS

Muntjac were the most consumed and most preferred prey by dholes in Southeast Asia, regardless of land cover type, prey diversity, and pack sizes. Consequently, muntjac and other small ungulates are now likely critical for conserving several remaining dhole populations in Southeast Asia, especially those in closed evergreen forests where dholes live in relatively small packs. In protected areas where dholes occur, we recommend that managers monitor muntjac populations to ensure that dholes have an adequate prey base. If muntjac numbers are low or declining, then law enforcement activities, such as snare removal and number of patrols, should increase to help stabilize and improve prey numbers. To conserve or increase dhole populations in open deciduous forests, we recommend restoring populations of large cervids (e.g., Eld's deer) because this would increase the abundance and availability of larger preferred prey species in ecosystems where dholes form larger packs. In Laotian protected areas where livestock predation by dholes is a concern in local communities, we recommend that managers encourage all villagers to remove livestock from the park during the dry season, or improve livestock guarding practices. These changes in herd management are likely to significantly reduce predation on livestock, and facilitate better coexistence between dholes and humans.

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