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The diet, prey selection, and activity of dholes (*Cuon alpinus*) in northern Laos

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Although Southeast Asia is one of the last strongholds of endangered dholes (*Cuon alpinus*), or Asiatic wild dogs, little is known about dhole ecology in this region. We used scat collections, prey surveys, and camera-trap data to determine the diet, prey selection, and activity of dholes in a national protected area in northern Laos. Results showed that dhole diets were dominated by ungulates (87% of biomass consumed), with additional prey including other carnivores (6%) and rodents < 1 kg (6%). Concerning individual prey species, only muntjac (*Muntiacus*, 45%) and sambar (*Rusa unicolor*, 33%) contributed $>7\%$ of biomass consumed. Dholes were not random in their consumption of ungulates, because muntjac (20–28 kg) and sambar (185 kg) were selectively consumed over medium-sized (75- to 85-kg) ungulates. Dholes were almost exclusively diurnal, and their activity pattern was significantly different (all $P < 0.003$) from that of all ungulate species except wild pigs (*Sus scrofa*). Overall, prey selection by dholes appeared to be more influenced by social behavior and terrain use of ungulates, rather than by body size or activity of ungulates. In tropical forests of northern Laos, dholes focused predation on relatively few species during diurnal hours, suggesting the management of muntjac and sambar may be important for conserving dhole populations in the region.

Key words: activity, Asiatic wild dog, *Cuon alpinus*, dhole, diet, Laos, prey selection, scat analysis

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The dhole (*Cuon alpinus*), or Asiatic wild dog, is classified as endangered by the International Union for Conservation of Nature after exhibiting severe declines in its numbers and distribution during the past 50 years (Durbin et al. 2004). Reasons for its decline are unclear, but are thought to be related to human persecution, severe decreases in natural prey, and destruction of habitat. The current distribution of dholes is restricted primarily to South and Southeast Asia, although populations may still be declining in these areas (Durbin et al. 2004). Despite being one of the last strongholds of dholes, little information exists from Southeast Asia regarding the ecology of dholes.

The dhole (10–20 kg—Durbin et al. 2004) is 1 of only 3 canid species with specialized morphological and behavioral adaptations for an exclusively carnivorous diet, termed hypercarnivory (Van Valkenburgh 1991). So whereas most canids have dental adaptations for omnivorous diets, dholes have enhanced slicing teeth and reduced number and size of molars, restricting their diets to pure flesh (Van Valkenburgh 1991). Behavioral traits associated with hypercarnivory include forming exceptionally large packs (often >10 members—Johnsingh 1982) to more efficiently hunt and consume large numbers of prey. Hypercarnivory also results in relatively large litters (often >10 pups/litter), and consequently dholes have more mammae (12–16) than any other canid species (Nowak 1999). However, these exceptionally large litters likely put severe limitations on minimum pack sizes. For example, dholes might need to maintain pack sizes >7 adults to successfully raise young, because smaller packs are not efficient enough to feed and protect such large litters (Johnsingh 1982). Because of the requirements of large pack sizes and hypercarnivorous diets (requiring high numbers of ungulates), the minimum land requirements for a sustainable dhole population are probably larger than for any other Asian mammal. For example, populations of dholes require 5 times more land area than populations of tigers (*Panthera tigris*) for long-term persistence, and consequently dholes have disappeared from more reserves than have tigers (Woodroffe and Ginsberg 1998). That habitat loss and fragmentation, along with poaching of wildlife, remain serious problems in Southeast Asia (Durbin et al. 2004) indicates that greater attention should be paid to dhole populations in the region because they likely face a high risk of extirpation.

Most information on dholes comes from studies carried out in tropical dry and moist deciduous forests in southern India. In those areas, chital (*Axis axis*) were the dominant prey item (Andheria et al. 2007; Johnsingh 1992; Karanth and Sunquist 1995; Venkataraman et al. 1995). Karanth and Sunquist (1995) concluded that dholes preferred prey weighing 31–175 kg, likely because this was energetically the optimal prey size for dholes and their relatively large packs. In central India and Bhutan, dholes were found to prey primarily on sambar (*Rusa unicolor*—Borah et al. 2009; Thinley et al. 2011), which were larger (approximately 185 kg) than typical prey from southern India. Interestingly, only 2 studies have determined dhole diets in moist, tropical, evergreen forests in Southeast Asia, and both found small ungulate species such as red muntjac (*Muntiacus muntjak* [20–28 kg]—Grassman et al. 2005) or mouse deer (*Tragulus* [2–5 kg]—Kawanishi and Sunquist 2008) to be the dominant prey item. Kawanishi and Sunquist (2008) concluded that dholes may live in relatively small packs in the dense tropical forests of Malaysia, and therefore are able to prey primarily on small ungulates. However, ungulate densities were not determined by Grassman et al. (2005) and Kawanishi and Sunquist (2008), therefore it was not known if dholes preferred small ungulates, or only consumed small species as alternative prey because numbers of larger ungulates were reduced due to poaching or other factors. Clearly, more information is needed on the diets of dholes in Southeast Asia, especially whether dholes selectively prey upon certain ungulate species. Such information will be important because management and enhancement of preferred prey may be essential for the long-term conservation of dholes in the region.

We studied the diets, prey selection, and activity of dholes in a national protected area in northern Lao People's Democratic Republic, hereafter Laos. We were interested in determining what species would be the dominant prey of dholes in our site, especially because chital and mouse deer (i.e., dominant prey identified in other studies) were absent from our region. We also were interested in what prey species were selectively preyed upon by dholes, especially because human hunting of wild ungulates is common in the region (Johnson et al. 2006). Consequently, preferred prey of dholes may need to managed or protected from human hunting to better conserve local dhole populations. Finally, we also compared activity patterns between dholes and the ungulate species, because previous research showed that activity of dholes was similar to that of their main prey (Karanth and Sunquist 2000; Kawanishi and Sunquist 2008). We predicted that dholes would selectively prey upon sambar, Chinese serow (*Capricornis milneedwardsii*; hereafter serow), and wild pig (*Sus scrofa*), because these species were the typical prey size for dholes in India. We also predicted that activity of dholes would be similar to that of their most preferred prey.

Materials and Methods

This paper was part of a larger study that focused primarily on determining the abundance of tigers and their prey in a protected area in Laos (Johnson et al. 2006; Vongkhamheng 2011). Scat collections, camera trapping, and occupancy sampling were the primary methods used to collect data. Extensive collections of scats, and subsequent confirmation of scats to species by genetic analysis, allowed us to conduct post hoc investigations of the diet, prey selection, and activity of dholes. We followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) during our research.

Study area.—We conducted research in the Nam Et-Phou Louey (NEPL) National Protected Area in northern Laos (5,950 km^2; Fig. 1). Elevation in NEPL ranges from 400 to 2,288 m, and vegetation is dominated by mixed evergreen–deciduous forest up to 1,500 m, transitioning into evergreen forest at 1,500–1,800 m, with interspersion of beech (*Fagus*) and *Rhododendron* above 1,800 m (Davidson 1998). About 91% of the area has slopes >12%. Annual rainfall (mainly May–October) is 1,400–1,800 mm, and temperatures range from 5°C (December–February) to 30°C (April–July). Other large (>15-kg) carnivore species recorded in NEPL include the tiger, leopard (*Panthera pardus*), clouded leopard (*Neofelis nebulosa*), Asiatic black bear (*Ursus thibetanus*), and sun bear (*Helarctos malayanus*—Johnson et al. 2006). Smaller carnivores in NEPL are described by Johnson et al. (2009). Wild ungulate species recorded in NEPL include gaur (*Bos frontalis*), sambar, serow, wild pig, and muntjac (primarily red muntjac—Johnson et al. 2006).

Diet analysis and prey selection.—The diet of dholes was determined by analysis of scats (i.e., feces) that were opportunistically collected by researchers and park staff in NEPL from December 2005 to May 2010, which corresponded to approximately 24 months before and 24 months after major prey surveys in NEPL (see below). Samples were collected by research teams during surveys for tigers and their potential prey (Vongkhamheng 2011) and opportunistically by park staff during routine patrolling. Because packs of dholes hunt, feed, and often defecate together in latrines (Durbin et al. 2004; Johnsingh 1982; Karanth and Sunquist 1995; Thinley et al. 2011), we sampled only 1 scat from each latrine to help ensure scats were from independent feeding events. For each scat, the scat diameter, date, and global positioning system location were recorded. Up to 10 g of each scat were sent to the Sackler Institute for Comparative Genetics, American Museum of Natural History (New York, New York) for species identification based on mitochondrial DNA analysis. Remaining parts of the scats were washed in a laboratory, and

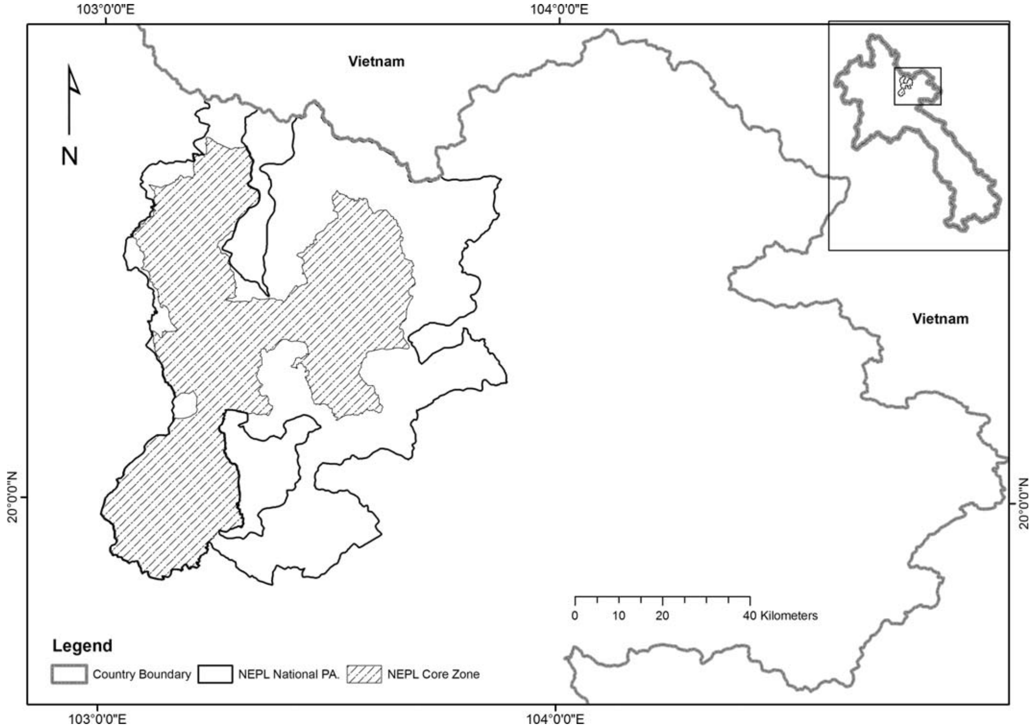

Fig. 1.—Location of the Nam Et-Phou Louey National Protected Area in northern Laos.

hair samples from each scat were identified to species by examining the structures of the cuticle, medulla, and cross sections under a microscope, and comparing those to a reference collection of hairs from known species.

Results from scat analysis were quantified in terms of both the percent biomass consumed and the frequency of occurrence (i.e., percentage of scats containing a particular food item). The percent biomass consumed is ecologically the most relevant parameter (Klare et al. 2011), and for this we used the linear regression model ($y_i = 0.439 + 0.008x_i$) developed for gray wolves (*Canis lupus*) by Weaver (1993) to calculate biomass consumed of different prey species. In the model, x is the live body mass of prey, whereas y is the mass of prey per collected scat (*i*). Although Weaver's equation was applicable to prey sizes only 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 ~ 0.5 kg).

The mean live body mass of sambar and wild pig was taken from Karanth and Sunquist (1995) based on the mean live body mass of those species killed by dholes in India. The mean live body mass of other prey species was taken from Francis (2008) using the given adult body masses, or the mean of adult males or females if both were given. For serow and Asiatic black bears, a value of 40% of the mean body mass of adult females was used, assuming that dholes killed younger rather than adult individuals. The value of 40% was based on results in India (Karanth and Sunquist 1995), in which the mean body masses of individual sambar and wild pigs killed by dholes were 38 and 41%, respectively, of the mean body masses of adult females. Although consumption of black bears could have been from scavenging carcasses of adults, we decided to be conservative and assume their consumption was from predation on younger individuals, similar to that assumed for ungulates. Because civets often could not be identified to species, we used the mean of the adult body masses of the large Indian civet (*Viverra zibetha*; 8.5 kg) and the common palm civet (*Paradoxurus hermaphroditus*; 4 kg), because these were the 2 most common civet species on the study site based on the camera-trap data (Johnson et al. 2009). Because Francis (2008) did not list a body mass for the brush-tailed porcupine (*Atherurus macrourus*), we obtained that body mass from Nowak (1999). Finally, we assumed a live body mass of 0.5 kg for all rats and large rodents found in scats because these species often could not be identified to species.

To determine numbers of individual prey consumed per dhole per year, we used the equation modified from Jędrzejewska and Jędrzejewski (1998): $N_{\mathrm{prey}} = (\mathrm{DFI} \times \mathrm{B}_{\mathrm{prey}} \times n_{\mathrm{days}} \times 100)/\mathrm{BM}_{\mathrm{prey}}$, where N_{prey} is the number of prey individuals eaten per dhole, DFI is the daily food intake of dholes, $\mathrm{B}_{\mathrm{prey}}$ is the percent biomass consumed by dholes for a given prey species, n_{days} is the number of days (i.e., 365 days in our analysis), and $\mathrm{BM}_{\mathrm{prey}}$ is the mean live body mass of prey. The daily food intake per dhole was assumed, conservatively, to be 1.36 kg based on the mean body mass (16 kg) given for dholes (Durbin et al. 2004), and that carnivores in general consume approximately 8.5% of their body mass per day (Mukherjee et al. 2004). The mean live body masses of prey species were the same used to determine percent biomass consumed (see above).

To determine relative abundance of prey species, we focused only on ungulates because previous research showed ungulates were the primary prey of dholes in other areas (Durbin et al. 2004), which was consistent with the results of our study. To determine the relative abundance of wild ungulates, we used occupancy sampling based on the presence or absence of sign of each ungulate species along transects established throughout 2,100 km^2 of the core area of NEPL (Vongkhamheng 2011). A grid cell of 13 km^2 was used as a sampling unit, with 289 grid cells throughout the study area. Each grid cell consisted of 4 equal-sized subgrid cells of 3.25 km^2. The biological basis for this specification was that the expected size of the largest home ranges among ungulates would be 13 km^2 or smaller (Vongkhamheng 2011). Within each subgrid, 9 equally spaced destination points, at 600-m intervals, were placed for logistic convenience, and at least 5 of these points were sampled by researchers when making routes throughout the subgrids (Vongkhamheng 2011). This sampling design generated 40 spatial replicates for each 13-km^2 grid. Survey teams walked predetermined routes through each subgrid, thoroughly searching for and recording prey signs (i.e., fresh tracks and fresh dung). All surveys were conducted during the dry season between January and June 2008 (see Vongkhamheng [2011] for more details of study design and analysis).

We calculated Ivlev's electivity index D (modified by Jacobs [1974]) to assess which prey species were selected ($0 < D \leq 1$) and which were avoided ($-1 \leq D < 0$). We calculated D-values from data from both biomass consumed and individuals consumed, to determine if both methods showed similar trends. For each prey species, the D-value depends on which other species are included in the calculation, therefore, we calculated D-values only for ungulate species for which abundances were determined during prey surveys. Because D-values of rare species often are biased (e.g., a detection in 1 scat might lead to a D-value of +1, whereas no detection would lead a D-value of -1), we used only those species that were >5% of biomass consumed or constituted >5% of the respective biomass available (Klare et al. 2010). Consequently, D-values were not calculated for gaur. Percent values of biomass consumed, biomass available, and number of individuals consumed were adjusted to only consider muntjac, sambar, serow, and wild pig. To determine biomass available for each ungulate species, we multiplied adult female body masses (from Francis 2008) by abundance estimates.

To determine the activity patterns of dholes and their prey, we used data from camera-trap surveys that were conducted annually during the dry season from 2003 to 2007 (see Johnson et al. [2006] for more details). Camera traps were set along game trails (Johnson et al. 2006), and we assumed photographs of dholes and ungulates accurately represented their respective activity patterns. For dholes, we also included independent photographs up to 2011 to increase the sample size for this species. Each photo was identified to species and rated as a dependent or independent event following O'Brien et al. (2003). We examined the time stamped on the individual independent photos and grouped activity times for each species into daytime or nighttime periods based on whether they occurred before or after sunrise and sunset. Sample sizes were too low for dholes to conduct a more detailed analysis of activity patterns. Chi-square tests with Yates' correction were used to compare proportion of active locations between dholes and each ungulate species. There were too few photos of gaur ($n = 3$) to conduct a statistical analysis for this species. For comparison purposes, we also calculated activity of presumed human hunters in the reserve based on independent photographs.

RESULTS

We used 76 scats in our analyses that were confirmed by DNA to be from dholes. Of 167 total scats collected during the study, DNA was successfully extracted from 90.4% of the samples (Vongkhamheng 2011). Most (84%) scats from dholes contained only 1 prey item, whereas 12% of scats contained 2 prey items and 4% of scats contained 3 prey items. There were remains of at least 9 species in the scats, including 4 ungulate species. Ungulates comprised 87% of all biomass consumed, followed by other carnivores (6% of biomass consumed) and rodents <1 kg (6%; Table 1). Muntjac and sambar were the 2 most dominant prey items in terms of biomass consumed and frequency of occurrence in scats, and no other prey items comprised >7% of the dhole diet in terms of biomass consumed (Table 1). Dholes consumed more individual muntjac and sambar than all other prey species except rodents <1 kg (Table 1).

Concerning ungulate species in NEPL, the results from occupancy sampling analysis showed estimated abundances to be 3.19 wild pig/km^2, 0.36 sambar/km^2, 1.5 muntjac/km^2, 0.22 serow/km^2, and 0.02 gaur/km^2 (Vongkhamheng 2011). The percentage of ungulate prey biomass available to dholes was 68% wild pig, 19% sambar, 8% muntjac, and 5% serow. The biomass consumed by dholes did not reflect the biomass available, because dholes showed a strong selection for muntjac ($D = 0.84$) and sambar ($D = 0.45$), whereas wild pig and serow were selected against ($D = -0.93$ and -0.27, respectively; Fig. 2). Similarly, the number of prey species consumed by dholes did not reflect the numbers available, because dholes had a positive selection for only muntjac and sambar (Fig. 2). Dholes were more diurnal and less nocturnal than sambar ($\chi^2 = 13.844$, $P < 0.001$), muntjac ($\chi^2 = 17.580$, $P < 0.001$), and serow ($\chi^2 = 9.425$, $P = 0.002$), but not different from wild pigs ($\chi^2 = 2.745$, $P = 0.098$) or human hunters ($\chi^2 = 0.285$, $P = 0.593$; Fig. 3).

DISCUSSION

Contrary to our prediction, muntjac, the smallest available ungulate, was the most common prey species of dholes in terms of biomass consumed and frequency of occurrence in scats. Additionally, muntjac had the highest electivity value of any ungulate species in terms of both biomass and numbers consumed. Our results were similar to the only 2 previous

TABLE 1.—Diets of dholes (*Cuon alpinus*) in the Nam Et-Phou Louey National Protected Area in northern Laos. Results are based on scat samples ($n = 76$) confirmed by genetic analysis to be from dholes.

Species	Biomass consumed (%)	Frequency of occurrence (%)	No. consumed per dhole per year
Muntjac (*Muntiacus*)	45.1	55.3	9.2
Sambar (*Rusa unicolor*)	33.1	25.0	2.3
Wild pig (*Sus scrofa*)	6.5	7.9	1.0
Serow (*Capricornis milneedwardsii*)	2.7	4.0	0.4
Black bear (*Ursus thibetanus*)	0.7	1.3	0.1
Civets	2.2	4.0	1.7
Hog badger (*Arctonyx collaris*)	3.3	6.6	1.5
Brush-tailed porcupine (*Atherurus macrourus*)	0.8	2.6	1.4
Rodents <1 kg	6.6	11.8	54.6

studies of dhole diets in Southeast Asia, which found that dhole preyed primarily on small ungulates (Grassman et al. 2005; Kawanishi and Sunquist 2008). The above results are in contrast to studies from India and Bhutan, which showed that the prey selection and diets of dholes were dominated by large ungulates such as chital or sambar (Andheria et al. 2007; Borah et al. 2009; Johnsingh 1992; Karanth and Sunquist 1995; Thinley et al. 2011; Venkataraman et al. 1995). Reasons for differences in dhole diet and prey selection between the regions are not clear, but may be related to difference in habitat, prey diversity, and pack sizes of dholes. For example, smaller pack sizes of dholes may be more energetically advantageous in rain forests where large prey species are scarce, and thick vegetation favors stalk and ambush hunting techniques over cursorial hunting (Kawanishi and Sunquist 2008), resulting in prey selection for small-sized ungulates. Unfortunately, we could not determine pack sizes of dholes on our study site; therefore, future research is needed to confirm the relationships among pack sizes of dholes, prey selection, and habitat.

Sambar were the 2nd most dominant prey species of dholes on our study, and there was a positive selection for sambar compared to availability, although the selection was not as strong as for muntjac. Although adult sambar may weigh up to 260 kg (Francis 2008), research in India showed that the mean body mass of sambar killed by dholes was 70 kg (Karanth and Sunquist 1995), indicating dholes prey primarily on young sambar rather than adults. Sambar were the 1st or 2nd most consumed ungulate in studies from southern India (Andheria et al. 2007; Cohen et al. 1978; Johnsingh 1992; Venkataraman et al. 1995), central India (Borah et al. 2009), Bhutan (Thinley et al. 2011), Thailand (Grassman et al. 2005), and Laos (this study). Additionally, a previous study also found that sambar were selectively consumed compared to other ungulates (Venkataraman et al. 1995). Thus, regardless of region, habitat, and ungulate diversity, sambar consistently were shown to be important prey for dholes.

In contrast to our prediction, dholes selected against serow and wild pigs, indicating that body size of prey was not the primary factor determining prey selection. Thus, factors other than body size must influence prey selection by dholes. Of the 5 ungulate species recorded in NEPL, only wild pigs and gaur are considered to live in groups, because sambar, muntjac, and serow are primarily solitary except for mother–young associations (Francis 2008). We did not detect any consumption of gaur by dholes in our study. Similarly, in places where they were sympatric, previous research also showed that gaur were rarely preyed upon by dholes (Andheria et al. 2007; Cohen et al. 1978; Karanth and Sunquist 1995). Dholes likely avoided predation on wild pigs because of the group living and protective behavior of the latter (Johnsingh 1992), regardless

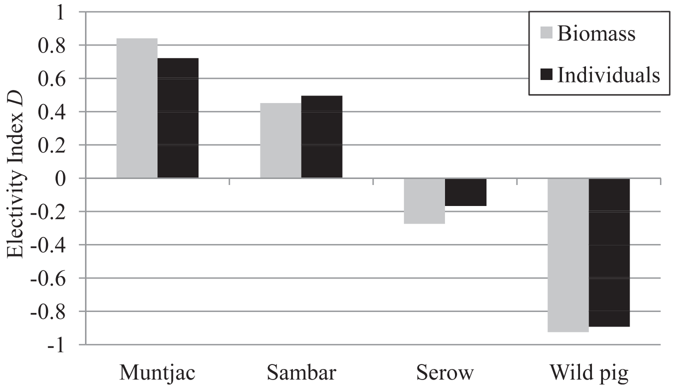

FIG. 2.—Ivelev's electivity index (*D*) of ungulates based on percent biomass consumed (Biomass) and number of individuals consumed (Individuals) by dholes in the Nam Et-Phou Louey National Protected Area, Laos.

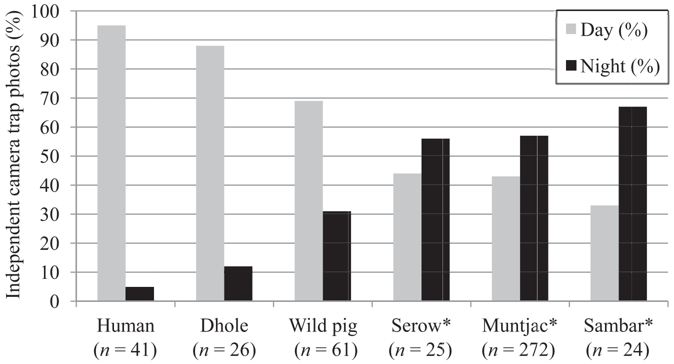

FIG. 3.—Activity patterns of dholes, presumed human hunters, and 4 ungulate species consumed by dholes in the Nam Et-Phou Louey National Protected Area, Laos. Activity patterns were based on the time of independent camera-trap photographs (n = number of photographs). Significant difference ($P < 0.05$) in activity pattern compared to dholes is indicated with an asterisk (*).

that wild pigs had the highest abundance of any ungulate species. Wild pigs also may be more dangerous to hunt and handle for dholes compared to other ungulates (Johnsingh 1992). Of 10 previous studies in southern Asia on dhole diets, only 1 (Grassman et al. 2005) found wild pigs to comprise >11% of dhole diets, despite wild pigs occurring on all study sites. Therefore, it appears that wild pigs generally are not important prey for dholes. Perhaps more surprising was that serow were not selectively consumed by dholes, despite serow being solitary and having a medium body size. Compared to muntjac and sambar, serow prefer steep terrain (Francis 2008), which is common throughout our study site. Dholes are cursorial hunters (Johnsingh 1992), and like most canids, are best adapted to pursuing prey on relatively flat terrain. Therefore, dholes may not have regularly hunted serow on steep terrain, especially if muntjac and sambar were more readily available on less-steep terrain.

Dholes were almost exclusively diurnal on our study site, which was similar to the activity reported for dholes in both India and other areas of Southeast Asia (Johnsingh 1982; Karanth and Sunquist 2000; Kawanishi and Sunquist 2008; Venkataraman et al. 1995). However, in contrast to both our prediction and the results of others (Karanth and Sunquist 2000; Kawanishi and Sunquist 2008), activity of dholes on our study site was significantly different from that of their main prey. In fact, the activity of dholes was most different from the 2 ungulates they selectively consumed (i.e., muntjac and sambar), whereas activity of dholes was most similar to that of wild pigs, the ungulate species that was most selected against. Although our results appear to be counterintuitive, circumstantial evidence suggests that muntjac on our study site may have become more nocturnal due to the hunting pressure from dholes. For example, muntjac were found to be primarily diurnal in Malaysia, in an area where dhole densities were extremely low compared to those of other large carnivores (Kawanishi and Sunquist 2004). In contrast, dholes in NEPL were the most common large (>15-kg) carnivore based on number of scats found and confirmed by DNA (Vongkhamheng 2011). An alternative explanation is that human hunting caused muntjac to become more nocturnal, because previous research showed ungulate activity can be influenced by human hunting (Kamler et al. 2007). Because activity of presumed human hunters was similar to that of dholes and almost exclusively diurnal, it was impossible to determine whether dholes or humans most influenced the activity of muntjac and other ungulates on our site. Regardless, the rather strict diurnal activity of dholes is in contrast to that of other large canids, such as gray wolves and African wild dogs (*Lycaon pictus*), which are capable of hunting both day and night (Mech 1992; Rasmussen and Macdonald 2012; Theuerkauf et al. 2003). Thus, the temporal niche of dholes apparently is more restricted than that found in other large canids.

Despite a diversity of ungulates and other potential prey species on our study site (Johnson et al. 2006), dholes preyed primarily on only 2 ungulate species. Additionally, dholes appear to be obligate diurnal hunters, which likely puts severe constraints on prey choice and resource use, at least compared to other large carnivores. Furthermore, prey selection by dholes was not just dependent on body size of ungulates, but apparently also social behavior and terrain use of ungulates. We conclude that the pressures of hypercarnivory and rather narrow niche breadth may be limiting factors for dhole populations in tropical forests of northern Laos. Consequently, the management of relatively few ungulate species, primarily muntjac and sambar, may be critical for dhole conservation efforts in the region.

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