

RESEARCH ARTICLE

Diet and prey selection of clouded leopards and tigers in Laos

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Funding information

Support for J. F. Kamler was provided by grants from the Kolmården Fundraising Foundation and Iris Darnton Foundation.

Abstract

In Southeast Asia, conservation of 'Vulnerable' clouded leopards (*Neofelis nebulosa*) and 'Endangered' tigers (*Panthera tigris*) might depend on the management of their preferred prey because large felid populations are limited by the availability of suitable prey. However, the diet of clouded leopards has never been determined, so the preferred prey of this felid remains unknown. The diet of tigers in the region has been studied only from one protected-area complex in western Thailand, but prey preferences were not determined. To better understand the primary and preferred prey of threatened felids, we used DNA-confirmed scats and prey surveys to determine the diet and prey selection of clouded leopards and tigers in a hilly evergreen forest in northern Laos. For clouded leopards, the primary prey was wild pig (*Sus scrofa*; 33% biomass consumed), followed by greater hog badger (*Arctonyx collaris*; 28%), small rodents (15%), and mainland serow (*Capricornis sumatraensis*; 13%; hereafter, serow). For tigers, the primary prey was wild pig (44%), followed by serow (18%), sambar (*Rusa unicolor*; 12%), and Asiatic black bear (*Ursus thibetanus*; 10%). Compared to availability, serow was positively selected by both clouded leopards ($D = 0.69$) and tigers (0.61), whereas all other ungulate species were consumed in proportion to the availability or avoided. Our results indicate that clouded leopards are generalist predators with a wide prey spectrum. Nonetheless, mid-sized ungulates (50–150 kg) comprised nearly half of their diet, and were the preferred prey, supporting a previous hypothesis that the enlarged gape and elongated canines of clouded leopards are adaptations for killing large prey. Because serow was the only ungulate preferred by both felids, we recommend that serow populations be monitored and managed to help conservation efforts for clouded leopards and tigers, at least in hilly evergreen forests of Southeast Asia.

KEYWORDS

Lao PDR, mainland serow, *Neofelis nebulosa*, niche breadth, *Panthera tigris*

TAXONOMY CLASSIFICATION

Conservation ecology

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1 | INTRODUCTION

Of the 10 large (>15 kg) felids worldwide, 9 of them have exhibited significant range declines and now are a conservation concern (Sandom et al., 2018). Prey loss is one of the primary reasons for large-felid extinctions and range loss (Sandom et al., 2018), especially in the Indo-Malayan region (Sandom et al., 2017). Because large felid populations are limited by prey availability, a major consideration of large felid conservation should be to maintain an adequate abundance of suitable prey that would be targeted by the felids (Clements et al., 2014; Karanth et al., 2004). Preferred prey (i.e., those targeted relative to abundance) are likely critical for tigers and other large carnivore populations because they provide the right-sized food 'packets' that can be killed by females with relative safety and at a rate sufficient to raise cubs (Miller et al., 2014). Consequently, one of the main ecological drivers of tiger density across their range is the density of preferred prey (Miller et al., 2014). Overall, the carrying capacity of large carnivores can be better determined by the biomass of preferred prey, compared to total ungulate biomass (Hayward et al., 2007). Ultimately, determining preferred prey should be a priority for the conservation of large felids because management and enhancement of the preferred prey may be required for their persistence (Clements et al., 2014; Karanth et al., 2004).

In Southeast Asia, the numbers and distribution of mainland clouded leopards (*Neofelis nebulosa*) has declined dramatically during the last 30 years, resulting in fragmented and mostly isolated populations; consequently, this species is classified as 'Vulnerable' at the global level by the International Union for the Conservation of Nature (IUCN; Gray et al., 2021). The primary reasons for the decline are habitat loss and illegal hunting (D'Cruze & Macdonald, 2015), although prey depletion also might be a threat, especially in China and Indochina (Gray et al., 2021). Although conservation priority areas for clouded leopards have been determined in Southeast Asia based on their habitat preferences (Macdonald et al., 2019), no information exists regarding their preferred prey because dietary studies have not been conducted for this felid species.

Clouded leopards are the smallest of the big cats (i.e., Pantherinae), but they have skull and dental morphologies that set them apart from all extant felids. They have the longest relative canines and largest gape of any extant felid species (Figure 1), and other dental, jaw, and skull morphologies that approach those of primitive saber-toothed cats (Christiansen, 2006). These unique adaptations are probably related to major differences in killing behavior compared to other extant felids (Christiansen, 2006). Whereas most large felids subdue large prey with a suffocating throat bite, available evidence indicates clouded leopards can kill large prey with a powerful nape bite (Christiansen, 2006; Grassman Jr. et al., 2005; Rabinowitz et al., 1987). Pocock (1939) also speculated that due to their long canines and stocky build, clouded leopards seem best adapted to take large ungulate prey. Nevertheless, most observations concerning the predatory behavior of clouded leopards and their sister species, the Sunda clouded leopard (*Neofelis diardi*), seem to suggest that they mainly prey on primates and small ungulates



FIGURE 1 A yawning mainland clouded leopard demonstrates the longest relative canines and largest gape of any extant felid species (photograph by Christian Sperka Photography)

such as muntjac (*Muntiacus* spp.; Matsuda et al., 2008; Morino, 2010; Nowell & Jackson, 1996; Sunderland-Groves et al., 2021). In the most detailed description of clouded leopard diets to date, Grassman Jr. et al. (2005) found that clouded leopards in Thailand preyed on rodents, Sunda pangolin (*Manis javanica*), Bengal slow loris (*Nycticebus bengalensis*), and hog deer (*Axis porcinus*) based on 4 scats collected from captured clouded leopards and finding 2 presumed kills. More detailed information is needed about clouded leopard diets, especially for determining their preferred prey, which could aid conservation efforts given that prey depletion is a major threat for this species (Gray et al., 2021).

Tigers (*Panthera tigris*) are listed as 'Endangered' at the global level by the IUCN because of drastic reductions in their numbers and distribution across their range (Goodrich et al., 2015). The future of one of the least studied subspecies, the Indochinese tiger (*P. tigris corbetti*), is especially bleak because of recent extirpations in several countries and former source sites (Ash et al., 2020; O'Kelly et al., 2012; Rasphone et al., 2019). The Malayan tiger (*P. tigris jacksoni*), the only other tiger subspecies found in mainland Southeast Asia, also is experiencing a population crash and is heading toward extinction due to illegal killings and habitat loss (Ten et al., 2021).

The diet and prey selection of tigers has been determined from several sites in the Indian subcontinent and Russian Far East, and a review of dietary studies primarily from those regions showed that tigers preferentially preyed most on the wild pig (*Sus scrofa*) and sambar (*Rusa unicolor*; Hayward et al., 2012). However, the food habits of tigers in Southeast Asia are almost unknown. Dietary studies of the Indochinese tiger were only conducted in Thung Yai-Huai Kha Khaeng (TY-HKK) protected-area complex in western Thailand. The TY-HKK contains a seasonally dry habitat dominated by deciduous and mixed-deciduous forests, and 4 dietary studies there gave conflicting results. Two studies found tigers consumed mostly large (>150 kg) ungulates, including banteng (*Bos javanicus*), gaur (*B. gaurus*),

and sambar (Pakpien et al., 2017; Simcharoen et al., 2018), whereas the other 2 studies found that tigers consumed mostly smaller ungulates, such as wild pig and northern red muntjac (*Muntiacus vaginalis*; 20–28 kg; Prommakul, 2003; Rabinowitz, 1989). The diet of Malayan tigers has not been studied, and what little is known comes from a few scats and presumed kills of tigers from Taman Negara National Park (TNNP), Peninsular Malaysia, which showed that tigers preyed on sun bear (*Helarctos malayanus*; $n = 3$), domestic cattle (*Bos taurus*; $n = 1$), and Sunda pangolin ($n = 1$; Kawanishi & Sunquist, 2004). In contrast to TY-HKK, the TNNP contains hilly evergreen forests where large ungulate (>150 kg) densities are relatively low compared to that of smaller ungulates (Kawanishi & Sunquist, 2004). More information about tiger diets is needed from Southeast Asia to aid conservation efforts there, given that prey numbers limit tiger population size (Karanth et al., 2004), and prey depletion is a major threat to tigers (Goodrich et al., 2015). Obtaining dietary data from closed evergreen forests are especially important because, in contrast to most other areas, large ungulates might not be the main prey of tigers in this habitat type (Sunquist et al., 1991).

We used DNA-confirmed scats and prey surveys to determine the diet and prey selection of clouded leopards and tigers in a national park containing hilly evergreen forests in northern Lao People's Democratic Republic (hereafter, Laos). We predicted that clouded leopards would consume mostly primates and preferentially prey on muntjac, a common small ungulate found on the site (Johnson et al., 2006; Rasphone et al., 2019). Because large cervids and large bovids were relatively rare at this site (Johnson et al., 2006; Rasphone et al., 2019), we predicted that tigers would consume mostly wild pig, and that tigers would preferentially prey on wild pig and sambar, similar to that reported for tigers in other regions (Hayward et al., 2012).

2 | METHODS

2.1 | Study area

We conducted research in the Nam Et-Phou Louey National Protected Area (hereafter, NEPL) in northern Laos (5950 km², Figure 2). Elevation in NEPL ranges from 400 to 2288 m, and it contains rugged and steep terrain with 91% of the area having slopes >12%. The vegetation is dominated by mixed evergreen-deciduous forest up to 1500 m, transitioning into evergreen forest at 1500–1800 m, with interspersions of beech (*Fagus* spp.) and rhododendrons (*Rhododendron* spp.) >1800 m (Davidson, 1998). Annual rainfall is 1400–1800 mm, and temperatures range from 5°C (December–February) to 30°C (April–July). There are two main seasons: the rainy season (about 15 May to 31 October) and dry season (about 1 November to 14 May; Kamler, Thatdokkham, et al., 2020). The NEPL is known for its high biodiversity, especially carnivores and their prey (Johnson et al., 2006; Rasphone et al., 2019). Other felid species recorded in NEPL during the study include the Asian golden cat (*Catopuma temminckii*), leopard cat (*Prionailurus bengalensis*), and

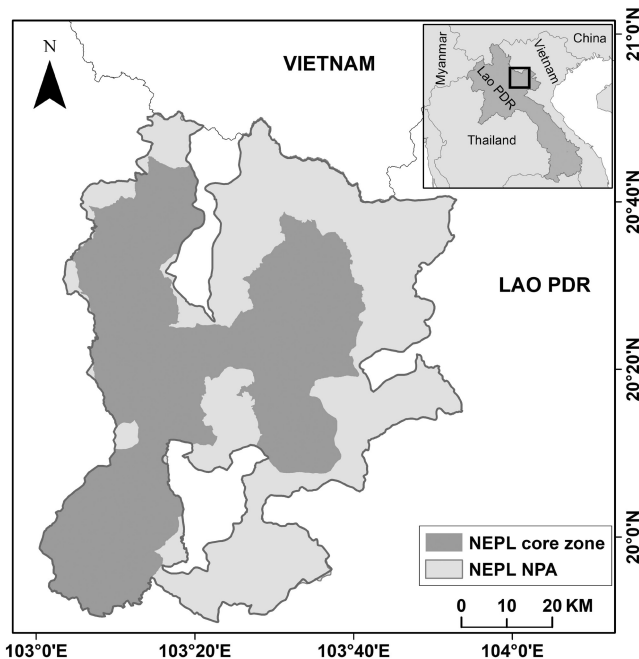


FIGURE 2 Location of Nam Et-Phou Louey National Protected Area in northern Laos

marbled cat (*Pardofelis marmorata*; Rasphone et al., 2019). Additional carnivore species include the dhole (*Cuon alpinus*), Asiatic black bear (*Ursus thibetanus*), and sun bear, as well as at least 13 small carnivore species (Rasphone et al., 2019). Prey species include wild ungulates such as gaur, sambar, mainland serow (*Capricornis sumatraensis*; hereafter, serow), wild pig, and at least two species of muntjac (primarily northern red muntjac), as well as 5 species of primates (Rasphone et al., 2019). The NEPL is officially divided into two zones: a totally protected core zone (3000 km²) where human activity (except for research and park management) is prohibited, and a peripheral managed-use zone (2950 km²) where villages occur and specified livelihood activities (e.g., collection of non-forest timber products, subsistence hunting of common species with traditional weapons) are permitted following park regulations (Figure 1). All of our research activities were carried out in the core zone.

2.2 | Scat analysis and prey selection

Diets of clouded leopards and tigers were determined by analysis of scats (i.e., feces) that were opportunistically collected on trails by researchers and park staff in NEPL from January 2008 to March 2012. Most scats were collected while conducting camera-trap surveys and grid-based occupancy surveys that covered the entire core zone (Johnson et al., 2016; Vongkhamheng et al., 2013); therefore, we assumed the collected scats represented a random sample of the felid populations. For each scat, the scat diameter (when possible), date, and GPS location were recorded, and then scats were stored in plastic bags with silica pouches to desiccate them. Up to 10 g of each scat were sent to the Sackler Institute for Comparative Genetics,

American Museum of Natural History (New York) for species identification based on mitochondrial DNA analysis (see Caragiulo et al., 2014 for methodological details). Remaining parts of the scats were washed over a sieve, dried for several days, and then contents were separated. 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. 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).

Results from scat analysis were quantified in terms of the percent biomass consumed because this method provides the most accurate estimate of carnivore diets using correction factors that account for differential digestibility of food items (Klare et al., 2011). Following the recommendations by Klare et al. (2011), we also included percent volume of food items, and the frequency of occurrence (i.e., percentage of scats containing a particular food item) to make our results more comparable to previous studies. To estimate biomass consumed, we followed Chakrabarti et al. (2016), who developed a generalized model (biomass consumed per collectable scat/predator weight = $0.033 - 0.025 \exp^{-4.284[\text{weight of prey killed/predator weight}]}$) based on feeding trials of several felid species ranging in size from the domestic cat (*Felis silvestris catus*) to the lion (*Panthera leo*). To determine if we obtained the minimum number of scats needed to adequately describe the diets of clouded leopards and tigers, we calculated a prey-species accumulation curve using the 'Vegan' package v. 2.5–6 with the function *specaccum* (Jaimes et al., 2018; Oksanen et al., 2019) in R version 4.0.5 (R Core Team, 2021). We calculated the expected mean prey richness and standard deviation with 10,000 permutations to obtain 95% confidence intervals (Gotelli & Colwell, 2001).

For the biomass consumed models (Chakrabarti et al., 2016), we used 17 kg for clouded leopards and 172.5 kg for tigers, which were the median of the weight ranges given by Nowell and Jackson (1996) and Francis (2008). For the prey weights of clouded leopards, we used half the weight of adult females for wild pig (37.5 kg) and serow (55 kg; Francis, 2008) because we assumed clouded leopards killed individuals ranging in size from young to adult females. We used a weight of 10.5 kg for the greater hog badger (*Arctonyx collaris*, hereafter hog badger; Francis, 2008), 2.75 kg for the Asiatic brush-tailed porcupine (*Atherurus macrourus*; Nowak, 1999), and 0.5 kg for rats (i.e., large murids). Because civet hairs often could not be identified to species, we used the mean of the adult weights of the large Indian civet (*Viverra zibetha*; 8.5 kg), common palm civet (*Paradoxurus hermaphroditus*; 2.5 kg), and masked palm civet (*Paguma larvata*; 4 kg), as these were the 3 most common civet species on the study site based on the camera trap data (Rasphone et al., 2019). We used a live weight of 0.5 kg for birds, assuming that clouded leopards consumed birds ranging in size from large songbirds (ca. 100 g) to red junglefowl (*Gallus gallus*; 1 kg). For the prey weights of tigers, we used 38 kg for wild pig and 212 kg for sambar, which was the mean weight of individuals killed by tigers in India (Karanth & Sunquist, 1995). We used

the adult weights of serow (135 kg), muntjac (24 kg) and stump-tailed macaque (*Macaca arctoides*; 10 kg; Francis, 2008), and the half the adult female weight for Asiatic black bears (50 kg), assuming tigers killed bears ranging in size from young to adult females. The weights for hog badgers and civets were the same as those used for clouded leopards. Based on the biomass of prey categories consumed, we calculated Levin's measure of niche breadth (B ; Krebs, 1989) for each felid species.

To determine prey selection of ungulate species consumed by clouded leopards and tigers, 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 average-sized individual within the population) by estimates of ungulate densities on our site. Ungulate densities were estimated in the core zone of NEPL in 2008 using a grid-based occupancy survey (Vongkhamheng et al., 2013), and results (individuals \pm SE/km²) were: muntjac, 1.50 ± 0.11 ; wild pig, 3.19 ± 0.15 ; sambar, 0.36 ± 0.01 ; serow, 0.22 ± 0.02 ; and gaur, 0.02 ± 0.003 . For the available biomass calculations, we used adult female weights of 20 kg for red muntjac, 75 kg for wild pig, 85 kg for serow, and 185 kg for sambar, which were based on lower weight given for each species by Francis (2008). Because D -values of rare species often are biased, we used only those species that were >5% of the biomass available (Klare et al., 2010); thus, D -values were not calculated for gaur. Following Laurenzi et al. (2016) who used the similar Ivlev's electivity index, we considered D -values to show preference if values were >0.30, and avoidance if values were <-0.30.

3 | RESULTS

There were 14 scats of clouded leopards and 21 scats of tigers that were confirmed by DNA analysis to be from those species, out of 361 scats collected. Mean (\pm SD) scat diameter was 2.1 ± 0.3 cm (range = 1.5–2.5 cm) for clouded leopards, and 4.0 ± 0.6 cm (range = 3.5–5.5 cm) for tigers. Most scats of clouded leopards (11/14) and tigers (17/21) were collected during the dry season. For clouded leopards, a majority of scats (8/14) contained 1 prey item, whereas remaining scats contained 2 or 3 prey items. Overall, we identified 7 prey species in their scats, including 2 ungulate species and at least 2 carnivore species (Table 1). Ungulates comprised 46% of all biomass consumed, followed by carnivores (33%) and rodents (18%, Table 1). Wild pig was the most dominant prey item (33% of biomass consumed), followed by hog badger (28%), small rodent (15%), and serow (13%), whereas no other species was >10% (Table 1). The prey accumulation curve for clouded leopards showed that an asymptote was not yet reached for the simulated data, although an asymptote was reached at 11 scats for the actual data (Figure A1).

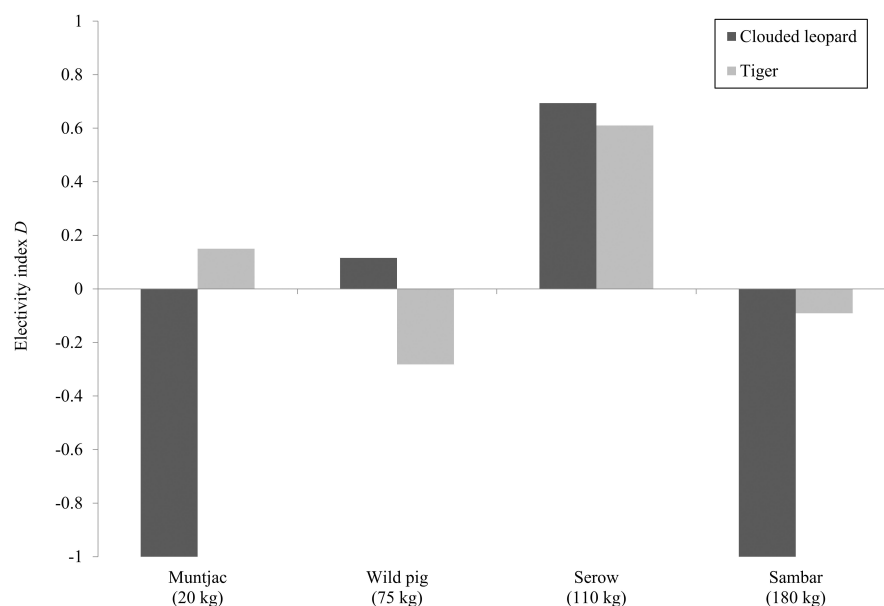
For tigers, a majority of scats (14/21) contained 1 prey item, whereas remaining scats contained 2 or 3 prey items. Overall, we identified 8 prey species in their scats, including 4 ungulate species and at least 3 carnivore species (Table 1). Ungulates comprised 81% of all biomass consumed, with carnivores being the only other

TABLE 1 Diet composition expressed as percentage of ingested biomass (Bio), percentage of scat volume (Vol), frequency of occurrence per scat (Occ), and dietary niche breadth (B) of clouded leopards and tigers in Nam Et-Phou Louey National Protected Area, Laos, 2008–2012

Prey category	Clouded leopard (n = 14 scats)			Tiger (n = 21 scats)		
	Bio	Vol	Occ	Bio	Vol	Occ
Ungulate	46.1	33.3	35.7	81.1	74.6	85.7
Wild pig (<i>Sus scrofa</i>)	33.3	23.8	28.6	43.8	44.0	52.4
Mainland serow (<i>Capricornis sumatraensis</i>)	13.3	9.5	14.3	18.0	13.1	19.0
Sambar (<i>Rusa unicolor</i>)	0.0	0.0	0.0	12.2	8.7	14.3
Muntjac (<i>Muntiacus</i> spp.)	0.0	0.0	0.0	7.2	8.7	14.3
Carnivore	32.7	25.0	28.6	17.5	23.0	33.3
Greater hog badger (<i>Arctonyx collaris</i>)	28.4	21.4	28.6	5.6	9.5	14.3
Civet ^a	4.2	3.6	7.1	2.4	4.8	4.8
Asiatic black bear (<i>Ursus thibetanus</i>)	0.0	0.0	0.0	9.6	8.7	14.3
Macaque (<i>Macaca</i> spp.)	0.0	0.0	0.0	1.4	2.4	4.8
Rodent	18.1	35.2	50.0	0.0	0.0	0.0
Brush-tailed porcupine (<i>Atherurus macrourus</i>)	3.1	3.6	7.1	0.0	0.0	0.0
Small rodent (Muridae)	14.7	31.6	50.0	0.0	0.0	0.0
Bird	3.0	6.4	14.3	0.0	0.0	0.0
Niche Breadth B	4.27			3.89		

^aProbably the common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*), and/or large Indian civet (*Viverra zibetha*).

FIGURE 3 Jacobs' (1974) electivity index (*D*) of ungulates based on percent biomass consumed by clouded leopards and tigers in Nam Et-Phou Louey National Protected Area, Laos, 2008–2012. Body mass of each species represents the adult female body mass reported by Francis (2008)



significant prey group consumed (18%; Table 1). Wild pig was the most dominant prey item (44% of biomass consumed), followed by serow (18%), sambar (12%), and Asian black bear (10%), whereas no other species was $\geq 10\%$ (Table 1). The prey accumulation curve for tigers approached an asymptote after 19 scats for the simulated data (based on upper limit of 95% CI's), and an asymptote was reached at 15 scats for the actual data (Figure A2).

The biomass of ungulates consumed by clouded leopards and tigers did not reflect the biomass available because both felids showed a preference for serow ($D = 0.69$ and 0.61 , respectively; Figure 3). Clouded leopards showed no selection for wild pig (0.12),

and a strong avoidance of both muntjac and sambar (-1.0 for both; Figure 23). Tigers showed no selection for muntjac (0.01), sambar (-0.09), and wild pig ($D = -0.28$, Figure 3). Overall, niche breadth values (B) were slightly higher for clouded leopards (4.27) compared to tigers (3.89 , Table 1).

4 | DISCUSSION

The diet of clouded leopards did not include primates or muntjac, which did not support our prediction. The lack of primates in our

sample of the clouded leopard scats was surprising, given that previous studies assumed that clouded leopards and Sunda clouded leopards were major predators of primates (Matsuda et al., 2008; Morino, 2010; Nowell & Jackson, 1996; Sunderland-Groves et al., 2021). Although we did not determine primate densities on our study site, four macaque species were present on our study site (Rasphone et al., 2019), and overall macaques were relatively abundant based on the camera-trap data (Johnson et al., 2006; Rasphone et al., 2019). Perhaps predation on primates was low in NEPL because macaques exhibit group defense and have formidable defense weaponry (i.e., large canines) to deter predation. Muntjac had the second highest density of all ungulates in NEPL (Vongkhamheng et al., 2013), yet they were not detected in clouded leopard scats. This was surprising given that concurrent studies showed that muntjac were 49% of the dhole diet and 22% of the Asian golden cat diet in NEPL (Kamler, Inthapanya, et al., 2020; Kamler, Thatdokkham, et al., 2020). Clouded leopards are similar in size to muntjac, so we assumed that if they preyed on ungulates, they would focus on muntjac similar to that shown for the other mid-sized carnivores, but this was not supported by our results.

Instead of relatively small prey, nearly half of the clouded leopard diet was comprised of medium-sized (50–150 kg) ungulates. Overall, wild pig was the primary prey of clouded leopards, whereas serow was the only ungulate preferred based on availability. Preference for serow by clouded leopards was unique among the other sympatric carnivores because concurrent dietary studies showed that neither dholes nor Asian golden cats preferentially consumed serow (Kamler et al., 2012; Kamler, Inthapanya, et al., 2020; Kamler, Thatdokkham, et al., 2020). Serow might even have influenced the activity patterns of clouded leopards, because a recent study in NEPL showed that clouded leopard had high activity overlap with serow ($\Delta = 0.75$), compared to lower activity overlap with northern red muntjac (0.65), squirrels (0.63), wild pig (0.60), birds (0.53), and 4 macaque species (0.41–0.52; Rasphone et al., 2020). Previous research has shown that felids often synchronize their activity to that of their main prey (Foster et al., 2013; Nagy-Reis et al., 2019; Yang et al., 2018). Interestingly, clouded leopards weigh 11–23 kg (Francis, 2008; Nowell & Jackson, 1996), so they overlap the 21.5–25 kg weight range where carnivores shift from small prey (less than half of carnivore mass) to large prey (near or greater than predator mass; Carbone et al., 1999), indicating clouded leopards taking large prey is consistent with carnivore energetic models. Although we could not determine if clouded leopards were feeding on adult or young ungulates, they mostly consumed medium-sized ungulate species when more abundant and smaller ungulate species were available is significant. Serow were not likely scavenged by clouded leopards because concurrent dietary studies in NEPL showed that serow was consumed in minimal amounts by dholes (6% of diet; Kamler, Thatdokkham, et al., 2020), Asian golden cats (1%; Kamler, Inthapanya, et al., 2020), and leopard cats (0%; Kamler, Inthapanya, et al., 2020), suggesting that serow carcasses were not readily available to carnivores on the study site. Overall, our results support the hypothesis by Pocock (1939) and Christiansen (2006) that the

elongated canines, large gape, and stocky build of the clouded leopard are adaptations to regularly take prey much larger than their own body size.

Hog badgers were the second most important prey item of clouded leopards, and overall carnivores comprised nearly one third of the clouded leopard diet, which was unexpected. Regarding other carnivores as prey, there was one previous report of a clouded leopard preying on a binturong (*Arctictis binturong*; Lam et al., 2014), and one previous report of a Sunda clouded leopard preying on a common palm civet (Rabinowitz et al., 1987). Greater hog badgers (7–14 kg; Francis, 2008) overlap in weight with clouded leopards, so it was somewhat surprising that clouded leopards fed more on this carnivore species compared to smaller carnivores species, such as the 4 civet species which are relatively abundant and widespread in NEPL (Rasphone et al., 2019). Perhaps their elongated canines and stocky build allows clouded leopards to regularly predate on similarly sized carnivores, which, based on optimal foraging theory, would be more energetically profitable than feeding on smaller carnivores, assuming that handling time is similar (MacCracken & Hansen, 1987). Hog badgers were not likely scavenged by clouded leopards because concurrent dietary studies in NEPL showed that hog badgers were consumed in minimal amounts by dholes (3% of diet; Kamler, Thatdokkham, et al., 2020), Asian golden cats (4%; Kamler, Inthapanya, et al., 2020), and leopard cats (0%; Kamler, Inthapanya, et al., 2020), suggesting that hog badger carcasses were not readily available to carnivores on the study site.

Small rodents were frequently consumed by clouded leopards in NEPL, as they were found in 50% of all clouded leopard scats. Nonetheless, small rodents contributed less to the biomass consumed by clouded leopards compared to ungulates and other carnivores. Small rodents reportedly were consumed by clouded leopards in Thailand (Grassman et al., 2005), so clearly small prey are regularly consumed by clouded leopards despite their apparent adaptations for killing large prey. Because clouded leopards overlap the 21.5–25 kg weight range that signals a major shift in carnivore diets, this species can energetically sustain itself on both large and small prey, unlike larger felids that are more energetically restricted to large prey (Carbone et al., 1999; Miller et al., 2014). Perhaps by having a body size that is capable of consuming both large and small prey, clouded leopards can coexist within diverse felid communities because they are able to reduce prey competition with large apex felids as well as small felids. Our results support this hypothesis because the clouded leopard had a relatively high dietary niche breadth that included a wide spectrum of prey sizes ranging from 0.5 kg to >100 kg.

Ungulates comprised 81% of the tiger diet, and wild pig were the most common prey item, which supported our prediction. In fact, wild pig was a higher component of the tiger diet in NEPL (34%) than in previous studies in TY-HKK, Thailand, where wild pig comprised 2–11% of the tiger diet (Pakpien et al., 2017; Prommakul, 2003; Rabinowitz, 1989; Simcharoen et al., 2018). Higher consumption of wild pig in NEPL probably was related to the scarcity of large bovids and sambar, as the latter two typically were the main prey of tiger in TY-HKK (Pakpien et al., 2017; Prommakul, 2003; Simcharoen et al., 2018). Despite the

high consumption, wild pig was not preferred prey of tigers in NEPL, which did not support our prediction. Similarly, sambar was consumed by tigers in NEPL, but it was not preferred prey, which also did not support our prediction. Our results are in contrast to other regions where wild pig and sambar were found to be the most preferred prey of tigers (Hayward et al., 2012).

Unexpectedly, serow was the second most important prey of tigers in NEPL, and the only preferred ungulate prey. To our knowledge, only one previous study reported that tigers consumed serow; in TY-HKK serow comprised 1 of 150 tiger kills (Pakpien et al., 2017). The body mass of serow (110–160 kg; Francis, 2008) is within the preferred prey weight range of tigers (60–250 kg; Hayward et al., 2012); thus, it was not surprising that tigers selectively consumed an ungulate species of this size. However, it was surprising that tigers selected serow instead of wild pig and sambar, because the latter two species also are within the preferred weight range of tigers and both are considered the tiger's most preferred prey in Russia and the Indian subcontinent (Hayward et al., 2012). Serow are rare or absent in Russia and the Indian subcontinent, whereas in Southeast Asia this species is somewhat widespread, especially in closed evergreen forests with rugged terrain (Phan et al., 2020) such as NEPL. When all three ungulate species are sympatric, we speculate that tigers prefer serow because this species is solitary and has less defense weaponry compared to wild pig and sambar; thus, serow potentially could be easier to stalk and safer to handle compared to the group-living wild pig and sambar. Also, because serow use more rugged and steep terrain compared to sambar and wild pig, then serow might have been more accessible to tigers if the latter used a hunting strategy that took advantage of this terrain. Prey accessibility has been shown to be more important than prey numbers regarding habitat selection and hunting strategy of large felids (Balme et al., 2007; Rostro-García et al., 2015).

Carnivores comprised 17% of the tiger diet in NEPL, mainly Asiatic black bears but also hog badgers and civets. Previous reviews found that tigers regularly consumed bears in the Russian Far East (Seryodkin et al., 2018), as well as other areas of Asia including Southeast Asia (Naing et al., 2019). Thus, it was not surprising to find bears in the tiger diet in NEPL, although at 10% of diet, bears appear to be more important prey to tigers in Southeast Asia than was previously assumed, at least in closed evergreen forests. Limited data from Peninsular Malaysia support this conclusion, because in the closed evergreen forests of Taman Negara National Park, bears comprised 3 of 5 tiger kills and scats that were found (Kawanishi & Sunquist, 2004).

In the core zone of NEPL, the estimated tiger population based on camera-trap surveys in 2003–2004 was 7–23 individuals (Johnson et al., 2006). Based on DNA analysis of tiger scats collected from 2008 to 2010, there were a minimum of 16 different individuals (Vongkhamheng, 2011), suggesting the tiger population remained low but stable in the NEPL core zone during our study. However, because of an exponential increase in illegal snaring that began after 2010 (Johnson et al., 2016), the tiger population quickly decreased to a minimum of 2 individuals by 2013, and soon thereafter likely

became extirpated (Rasphone et al., 2019). Nonetheless, most of our data were collected before the exponential increase in snaring, and we assume our results adequately represent tiger dietary habits in a low-density population occupying hilly evergreen forests.

A major limitation of our study was the low sample of scats for each felid species, especially for clouded leopards because the simulated data for their prey species did not reach an asymptote. Therefore, the lack of primates and muntjac detected in clouded leopard scats could have been an artifact of our low sample size. Pseudo-replication might affect small sample sizes from low density populations, although that was not likely the case in our study. For example, more detailed genetic analysis on the first 16 tiger scats collected found that they came from 16 different individuals (Vongkhamheng, 2011). For clouded leopards, a detailed camera-trap study from 2013 to 2017 estimated a density of 1.8 individuals/100 km² in our study site with a minimum of 41 different individuals detected and a high turnover of individuals between years (Rasphone et al., 2021); thus, the scats we collected over 4 years likely were not biased towards a few individuals. Interestingly, clouded leopards apparently do not defecate on trails to mark their territories (Rabinowitz et al., 1987), in contrast to other felids (Harmsen et al., 2010; Kamler, Inthapanya, et al., 2020; Rodgers et al., 2015), which may explain the low sample size in our study, and why no previous dietary studies were conducted on clouded leopards (i.e., researchers rarely, if ever, find scats of this species). Nevertheless, if male clouded leopards defecated on trails at a higher rate than females, our results could have been sex biased. Finally, because most scats from both felids were collected during the dry season, our results could have had a seasonal bias if predatory habits differed between the dry and rainy seasons. For example, ungulate birth pulses, rutting behavior, and migration might result in a seasonal variation in carnivore diets, including the tiger (Schaller, 1967). Nonetheless, a concurrent study of dhole diets in NEPL with a large sample size ($n = 165$ scats) showed there was no significant difference between the dry and rainy seasons (Kamler, Thatdokham, et al., 2020), suggesting seasonal differences in diets of tigers and clouded leopards in NEPL could have been minimal.

4.1 | Conservation implications

Our study represents the first ever dietary study of clouded leopards, and the first dietary study of tigers in Southeast Asia from hilly evergreen forests. Because serow was the only ungulate preferred by clouded leopards and tigers, this prey species likely is important for the conservation of both felids, at least in some areas of Southeast Asia. In protected areas containing hilly evergreen forests where clouded leopards or tigers occur, we recommend that park managers monitor serow populations to ensure that both large felids have an adequate population of their preferred prey. The mainland serow is classified as 'Vulnerable' at the global level by the IUCN because its populations are fragmented and in rapid decline due to poaching and habitat loss (Phan et al., 2020). Therefore, reintroductions or supplemental releases of serow might be necessary in areas

where serow populations have become decimated by poaching because scarcity of preferred prey can hamper the recovery of tigers and other large felids (Clements et al., 2014; Hayward et al., 2007; Karanth et al., 2004; Miller et al., 2014; Sandom et al., 2017, 2018). We recommend further research on the diets of clouded leopards and tigers in Southeast Asia, including larger sample sizes from all seasons and data from sites with different habitat and prey communities. Only by studying these felids in various ecosystems can we better understand their predatory niches and determine their ecological requirements.

AUTHOR CONTRIBUTIONS

Akhousanh Rasphone: Conceptualization (lead); formal analysis (lead); investigation (lead); methodology (lead); writing – original draft (lead). **Anita Bousa:** Methodology (equal); writing – review and editing (supporting). **Chantavy Vongkhamheng:** Methodology (equal); writing – review and editing (supporting). **Jan F Kamler:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (supporting). **Arlyne Johnson:** Funding acquisition (equal); project administration (supporting); writing – review and editing (supporting). **David Macdonald:** Funding acquisition (equal); writing – review and editing (supporting).

ACKNOWLEDGMENTS

We conducted the study under a Memorandum of Understanding between the Department of Forestry and the Wildlife Conservation Society. We thank the survey teams and staff, especially B. Xayavong for help with collecting data, and the government authorities in Houaphan and Luang Prabang provinces for the invitation to work in NEPL. We thank K. L. Nicholson, M. Franchini, and an anonymous reviewer for helpful comments that improved the paper.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Results of the analysis of individual scats are available via DRYAD: <https://doi.org/10.5061/dryad.w0vt4b8v5>.

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How to cite this article: Rasphone, A., Bousa, A., Vongkhamheng, C., Kamler, J. F., Johnson, A., & Macdonald, D. W. (2022). Diet and prey selection of clouded leopards and tigers in Laos. *Ecology and Evolution*, 12, e9067. <https://doi.org/10.1002/ece3.9067>

APPENDIX

FIGURE A1 Accumulation curve (gray line) of expected mean prey richness from clouded leopard scats collected in Nam Et-Phou Louey National Protected Area, Laos, 2008–2012. The bars represent 95% confidence intervals based on 10,000 permutations. The black line represents the actual accumulation of prey species based on scat content in the order in which scats were found

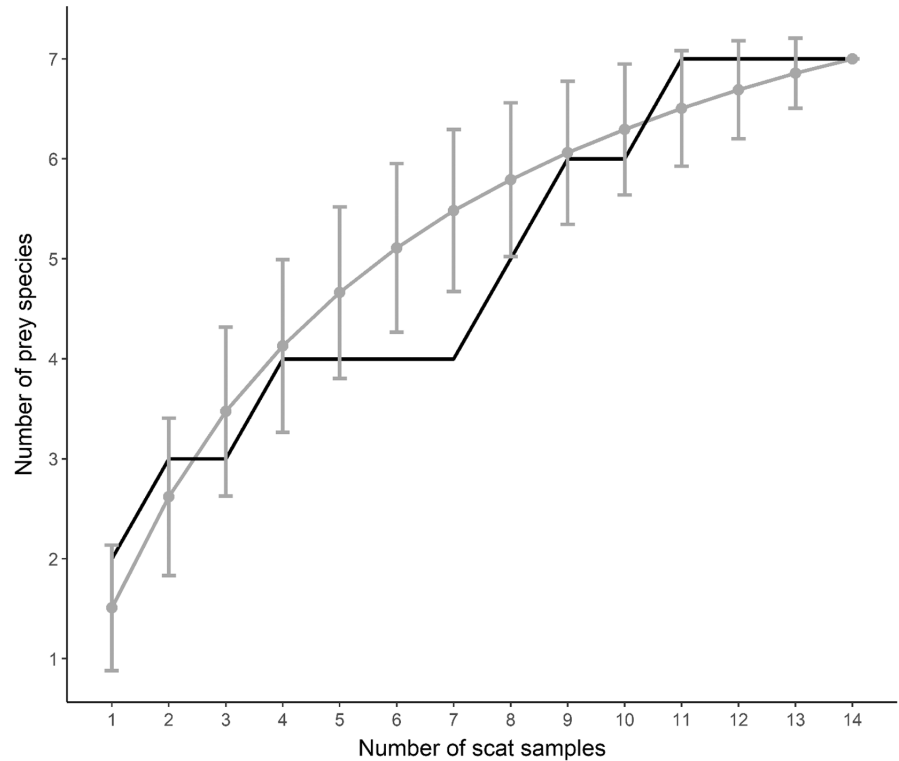


FIGURE A2 Accumulation curve (gray line) of expected mean prey richness from tiger scats collected in Nam Et-Phou Louey National Protected Area, Laos, 2008–2012. The bars represent 95% confidence intervals based on 10,000 permutations. The black line represents the actual accumulation of prey species based on scat content in the order in which scats were found

