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Jan F. Kamler
Wildlife Conservation Research Unit
Dept. of Zoology, Oxford University
The Recanati-Kaplan Centre, Tubney House
Abingdon Road, Tubney
Abingdon OX13 5QL
United Kingdom
Phone: (+44) 0-1865-611100; Fax: (+44) 0-1865-611101
E-mail: jan.f.kamler@gmail.com

RH: **KAMLER ET AL.—ASIAN GOLDEN CAT AND LEOPARD CAT IN LAOS**

Diet, prey selection, and activity of Asian golden cats and leopard cats in northern Laos

Jan F. Kamler*, Xaysavanh Inthapanya, Akchousanh Rasphone, Anita Bousa,
Chanthavy Vongkhamheng, Arlyne Johnson, and David W. Macdonald

Wildlife Conservation Research Unit, University of Oxford, Department of Zoology, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, United Kingdom (JFK, DWM)

Faculty of Science, National University of Laos, P.O. Box 7322, Vientiane, Lao People's Democratic Republic (XI)

Wildlife Conservation Society-Lao PDR Program, P.O. Box 6712, Vientiane, Lao People's Democratic Republic (AR, AB, CV, AJ)

Present address of XI: Forest Inventory and Planning Division, Department of Forestry, P.O. Box 2932, Vientiane, Lao People's Democratic Republic

Present address of AJ: Foundations of Success, 4109 Maryland Avenue, Bethesda, MD 20816, USA

**Correspondent: jan.f.kamler@gmail.com*

The Asian golden cat (*Catopuma temminckii*) occurs in small, declining, and highly fragmented populations throughout Southeast Asia, whereas the smaller leopard cat (*Prionailurus bengalensis*) is common and widespread. In contrast to leopard cats, little is known about the ecology of Asian golden cats, and resource partitioning between these species has not been studied. We used DNA-confirmed scats, camera-trap data, and prey surveys, to determine the diet, prey selection, and activity of Asian golden cats and leopard cats in a protected area in northern Laos. The two felids had different diets: Asian golden cats consumed mostly ungulates (35% biomass consumed), murid rodents (23%), and carnivores (15%), whereas leopard cats consumed mostly murid rodents (79%). Asian golden cats were not random in their consumption of ungulates, because muntjac (*Muntiacus* spp.) were selectively consumed over larger ungulates, indicating muntjac were preyed upon rather than scavenged. Dietary overlap between the two felid species was relatively low ($R_0 = 0.60$), and the dietary niche breadth of Asian golden cats ($B = 8.44$) was nearly twice as high as that of leopard cats (4.54). The mean (±SD) scat diameter was greater for Asian golden cats (2.1 ± 0.3 cm) than leopard cats (1.8 ± 0.2 cm), although diameters of leopard cat scats were considerably larger than previously assumed for this species. The felid species differed in their activity patterns, as Asian golden cats were diurnal whereas leopard cats were nocturnal, although they did not differ in their use of elevation, suggesting there was no habitat segregation. Overall, leopard cats appeared to coexist with Asian golden cats, a potential predator and competitor, by exhibiting dietary and temporal partitioning. Our results showed that muntjac were important prey of Asian golden cats, suggesting the management of muntjac might be important for conserving populations of Asian golden cats.

Key words: Activity overlap, biomass consumed, *Catopuma temminckii*, dietary overlap, food habits, Lao PDR, Nam Et-Phou Louey, *Prionailurus bengalensis*

The Asian golden cat (*Catopuma temminckii*; 12-15 kg; Francis 2008) and leopard cat (*Prionailurus bengalensis*; 3-5 kg; Francis 2008) are sympatric in Southeast Asia, although almost nothing in known about their resource partitioning and mechanisms of coexistence. Larger carnivores tend to dominate smaller carnivores, especially those that are taxonomically similar (Donadio and Buskirk 2006), therefore Asian golden cats should behaviorally dominate leopard cats. Among felids, interference competition has been well documented, including the killing of smaller felids by larger felids (Palomares and Caro, 1999; Kamler et al. 2015). Consequently, smaller felids should employ different mechanism to coexist with larger felids, including temporal, spatial, and dietary partitioning (Fedriani et al. 1999; Carvalho and Gomes 2004; Lucherini et al. 2009; Kamler et al. 2003, 2012b, 2013), although the degree of partitioning may depend on availability of food resources (Holt and Polis 1997; Kamler et al. 2007a). Thus, leopard cats likely employ one or more mechanisms to partition resources and coexist with the Asian golden cats, although this has never been investigated. Previous studies have shown that Asian golden cats are more diurnal than sympatric leopard cats (Grassman et al. 2005a, b; Johnson et al. 2009; Lynam et al. 2013; McCarthy et al. 2015b; Mukherjee et al. 2019;

Rasphone et al. In Press), indicating leopard cats might be using temporal partitioning to avoid Asian golden cats. However, the extent of dietary and habitat partitioning between leopard cats and Asian golden cats is unknown. In particular, dietary overlap often drives interference competition within trophic guilds (Palomares and Caro 1999), consequently dietary partitioning can be key to successful coexistence among carnivores (Tsunoda et al. 2017). Determining dietary and other resource partitioning between leopard cats and Asian golden cats therefore would help explain how the leopard cat coexists with a dominant competitor and potential predator. Determining the level of resource partitioning between Asian gold cats and leopard cats will enhance our knowledge not only of the ecology and behavior of each species, but also of the coexistence mechanisms employed by sympatric felids in South Asia, the most felid-rich region in the world (Luo et al. 2014).

Although the Asian golden cat once was widely distributed throughout Southeast Asia and southern China, this species now is restricted to highly fragmented and declining populations because of habitat loss and poaching, and is classified as Near Threatened by the IUCN (McCarthy et al. 2015a). Due to its low numbers and secretive nature, little is known about the ecology of the Asian golden cat. For example, only one study has determined the home range size of Asian golden cats (Grassman et al. 2005a). The density of Asian golden cats has never been determined, probably because this species typically lacks unique identification marks, although some populations exhibit polymorphism with individuals that have unique marks (Nijhawan et al. 2019). Several camera-trap studies have investigated its activity pattern, and concluded this species is arrhythmic or mostly diurnal (Grassman et al. 2005a; Haidir et al. 2018; Johnson et al. 2009; Lynam et al. 2013; McCarthy et al. 2015b; Mukherjee et al. 2019; Rasphone et al. in press; Ridout and Linkie 2009). The food habits of this species are poorly known, and are based on just a few dietary studies with low sample sizes. In Malaysia, 15 DNA-confirmed scats of Asian golden cats were analyzed; the results showed that they consumed mostly reptiles (7/15 scats), murids (7/15), and mouse deer (*Tragulus* spp.; 3/15; Kawanishi and Sunquist 2008). In China, 10 scats from Asian golden cats were analyzed using DNA analysis and metabarcoding, and most prey species were identified as rodents and birds, although at least traces of 3 ungulate species were detected (Xiong et al. 2017). In Malaysia, the stomach contents of four road-killed specimens examined by Lim (2002) included one each of rat, lizard, Asian palm civet (*Paradoxurus hermaphroditus*), and mouse deer. One confirmed scat from an Asian golden cat in Thailand contained a ground squirrel (*Menetes berdmorei*; Grassman et al. 2005a). Consequently, the dietary niche and predatory habits of this species remain unclear. For example, although ungulates were detected in diets of Asian golden cat, it was not known if they preyed on ungulates, or simply scavenged. The limited information available indicates Asian golden cats might rely primarily on small prey, such as small rodents and small reptiles, and possibly small (< 6 kg) ungulates, although there are anecdotal reports of Asian golden cats preying on larger ungulates (Nowell and Jackson 1996). Clearly, more information is needed on the diet of Asian golden cats, especially whether they regularly prey on medium- or large-sized ungulates, and if so, whether they selectively consume certain species. Such information is relevant, because conservation of carnivores often includes the management and enhancement of their preferred prey (Clements et al. 2014; Karanth et al. 2004).

The leopard cat has remained common throughout its distribution and has not exhibited any major range contractions; consequently, it is classified as Least Concern by the IUCN (Ross et al. 2015). Several investigators have studied the ecology of leopard cats, particularly the endangered subspecies on Japanese islands (Izawa et al. 2009; Hisano and Newman 2020). On mainland Asia, four studies have assessed the home range size of leopard cats (Rabinowitz 1990; Grassman 2000; Grassman et al. 2005b; Austin et al. 2007). Density estimates have been reported across 10 sites, ranging widely from 2 to 89 individuals/100 km^2 depending on the habitat (Bashir et al. 2013; Chua et al. 2016; Mohamed et al. 2013; Peterson et al. 2019; Rasphone 2018; Selvan et al. 2014; Srivathsa et al. 2015). The activity of leopard cats was found to be mostly arrhythmic or nocturnal (Austin et al. 2007; Bashir et al. 2014; Grassman 2000; Grassman et al. 2005b; Johnson et al. 2009; Lynam et al. 2013; McCarthy et al. 2015b; Mukherjee et al. 2019; Rasphone et al. in press). The diets of leopard cats have been reported from at least 12 studies (with > 20 sample sizes), excluding the Japanese islands, and rodents, primarily murids, were found to be the most important prey across studies (Table 1). Nonetheless, only 3 of 12 dietary studies confirmed using DNA analysis that the scats belonged to leopard cats (Table 1); the extent to which most previous dietary studies included scats of other sympatric small carnivores therefore is unknown. Previous research has shown that DNA analysis of scats is necessary to confirm species, because misidentification of carnivore scat is common based on size and shape, even by experts in the field (Baines et al. 2013; Janečka et al. 2008; Weiskopf et al. 2016). In particular, DNA analyses in two studies have shown that scats of leopard cats are often incorrectly identified in the field as belonging to larger felid species (Karmacharya et al. 2016; Khatoon et al. 2019), presumably because leopard cat scats often are larger than what field researchers anticipate.

We used DNA-confirmed scats and camera-trap surveys to study the dietary, activity, and elevational, overlap between Asian golden cats and leopard cats in a national protected area in northern Lao People's Democratic Republic, hereafter Laos. Because mouse deer, a small ungulate (1-5 kg; Francis 2008) reportedly consumed by Asian golden cats in other areas, was absent from our region, we assumed that ungulates would not be a significant part of their diet in our study site. Therefore, we predicted that both felids would consume mostly small mammals and exhibit high dietary overlap. If Asian golden cats did consume ungulates, we were interested in knowing whether ungulate species were selectively consumed, to determine preferred prey and conclude whether Asian golden cats were preying or scavenging. Based on previous studies, we also predicted that leopard cats would have low temporal and elevational overlap with Asian golden cats, as a means to partition resources and coexist with a larger competitor and potential predator.

MATERIAL AND METHODS

Study area.—We carried out the research in Nam Et-Phou Louey (NEPL) National Protected Area in northern Laos (5,950 km^2; Fig. 1). Elevation in NEPL ranges from 400 m 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* spp.) and rhododendrons (*Rhododendron* spp.) > 1,800 m (Davidson 1998). About 91% of the area has slopes > 12%. Annual rainfall (mainly May to October) is 1,400-1,800 mm, and temperatures range from 5°C (December-February) to 30°C (April-July). Other felid species recorded in NEPL include tiger (*Panthera tigris*), clouded leopard (*Neofelis nebulosa),* and marbled cat (*Pardofelis marmorata*; Rasphone et al. 2019). Additional carnivore species include the dhole (*Cuon alpinus*), Asian black bear (*Ursus thibetanus*), and sun bear (*U. malayanus*), as well as at least 13 small carnivore species (Johnson et al. 2009; Rasphone et al. 2019). Wild ungulate species recorded in NEPL include gaur (*Bos frontalis*), sambar (*Rusa unicolor*), mainland serow (*Capricornis sumatraensis*; hereafter, serow), wild pig (*Sus scrofa*), and 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 (Rasphone et al. 2019).

Diet analysis and prey selection.—Diets of Asian golden cats and leopard cats were determined by analysis of 88 scats (i.e., feces) that were collected from February 2010 to March 2012, while walking trails throughout the core zone of NEPL to conduct camera trap surveys. To increase sample size, we also included 18 scats that were opportunistically collected from February 2007 to December 2008 in NEPL by researchers and park staff during previous research activities and routine patrolling. Scats were collected during the dry season (December to May) because this is when nearly all field research is conducted, and scats last longer in the field because they are not washed away by rain. For each scat, the scat diameter (when possible), date, and GPS location, were recorded. We also recorded if scats were deposited singly, or in latrines containing multiple scats. If fresh scats were collected, they were allowed to air dry in the sun for ca. 3 days before processing. The dry weight of each scat was determined by weighing each scat after drying to the nearest 0.1 g (Baker et al. 1993). We took 2-10 g of flakes from the outer coating of scats, usually near the ends, and sent them 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). Thereafter, scats were washed in a sieve with 0.5 mm mesh to clean the undigested, macroscopic scat remainders. The scat remainders were dried on plates and then separated into different food categories that were identified using a reference collection. We visually estimated volume of each food item in scats to the nearest 5%. Food items that were considered trace (< 3% of scat) were excluded from analysis to minimize bias (Kamler et al. 2007b). For small (< 1 kg) mammals, it was not possible to identify remains to species based on hair structure, given the great diversity of small mammals in the area (Lunde and Son 2001) and their similarities in hair structure. We therefore classified small mammal remains to family based on tooth morphology either as Muridae, Sciuridae, Soricidae, or Tupaiidae. For Muridae teeth, we further grouped these as either large (≥ 2.0 mm) or small (< 2.0 mm) to represent rat-sized murids (hereafter rats; about 200 g body mass) and mouse-sized murids (hereafter mice; about 50 g), respectively. For larger mammals, hair samples from each scat were identified to species by examining the structures of the cuticle and medulla under a microscope, and comparing those to a reference collection of hairs from known species. We compared the mean diameter of DNA-confirmed scats between Asian golden cats and leopard cats using a *t*-test. To assist future researchers, we also compared the range of scat diameters among all carnivore species with DNA-confirmed scats to determine the amount of interspecific overlap in scat sizes.

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. We calculated two different estimates of biomass consumed based on previous feeding trials of mesofelids. For one biomass estimate, we followed Baker et al. (1993), who developed a model based on feeding trials on bobcats (*Lynx rufus*). For prey species < 4.5 kg, Baker et al. (1993) used a linear regression model ($y = 16.63 + 4.09x$) to calculate biomass consumed based on the weight of dried prey remains in scats. In the model, y

is the conversion factor (CF, or fresh mass of prey consumed [g] per gram of scat produced [dry weight]), whereas x is the live body weight of prey items (kg). Because Baker et al.'s (1993) equation was not relevant for prey > 4.5 kg, we used a correction factor of 30 for ungulates and larger prey species, which was based on the mean correction factor determined during a feeding trial for Eurasian lynx (*Lynx lynx*) when these were fed seven different-sized ungulates (Rühe et al. 2007). For the other biomass estimate, 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 lion (*Panthera leo*), leopard (*P. pardus*), jungle cat (*Felis chaus*), and domestic cat (*F. silvestris catus*). We considered the model developed by Chakrabarti et al. (2016) to be superior because it was applicable to felid species of all body sizes and included prey weight of all sizes. Consequently, we used the estimates of biomass consumed following Chakrabarti et al. (2016) in our paper when referring to the diets of Asian golden cats and leopard cats, unless otherwise noted. However, we also provided the results following Baker et al. (1993) in a table to enable comparisons to previous studies.

For both estimates of biomass consumed, we used 24 kg as the live weight of muntjac killed, which was the median of the weight range given by Francis (2008), because we assumed that mostly adult muntjac were preyed upon. We also used 24 kg as the live weight killed for all larger ungulates, assuming that mainly young (i.e., muntjac-sized individuals) of larger species were preyed upon by Asian golden cats. The hairs of civets could not be distinguished between Asian palm civet and the masked palm civet (*Paguma larvata*), therefore we used a live weight of 3.5 kg for civets because this was middle of the weight ranges given for both species by Francis (2008). We used a live weight of 10.5 kg for hog badger (*Arctonyx collaris*; Francis 2008), 2.75 kg for brush-tailed porcupine (*Atherurus macrourus*; Nowak 1999), and 160 g for

Tupaiidae (assuming most were *Tupaia belangeri*). For Soricidae, we assumed a live weight of 12 g, based on the body mass of *Crocidura fuliginosa*, a shrew that is common in the region (Parr et al. 2014). For small mammals, we assumed a live weight of 300 g for Sciuridae, 200 g for large Muridae (rats), and 50 g for small Muridae (mice), based on approximate weights of species within these groups that likely occupy our study site (Lunde and Son 2001). We assumed a live weight of 500 g for birds, assuming that the felids consumed birds ranging in size from small songbirds (ca. 10 g) to red jungle fowl (*Gallus gallus*; 1 kg). For the Chakrabarti et al. (2016) model, we used a body mass of 13.5 kg for Asian golden cats and 4 kg for leopard cats because these were the median of the weight ranges given by Francis (2008). We determined if there was a difference between felid species in the frequency of consumed prey items using chi-square contingency tables. For this analysis, we grouped prey into 6 broad categories: ungulates, carnivores, Muridae, Sciuridae, porcupine, and other. If a significant difference ($P < 0.05$) occurred, then we used Fisher's exact tests to determine which individual prey categories significantly differed between species. Based on the biomass of prey categories consumed, we calculated degree of dietary overlap between the two felid species using Horn's index of overlap (R_0; Krebs 1989) and also calculated Levin's measure of niche breadth (B; Krebs 1989) for each felid species.

To determine prey selection of ungulate species consumed by Asian golden cats, 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 (D) were estimated in the core zone of NEPL in 2008 using a grid-based occupancy survey (Vongkhamheng et al. 2013), and results (D ± SE km^{-}

^{2}) 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.

Activity pattern and elevation analyses.—To determine and compare activity patterns between Asian golden cats and leopard cats, we used data from camera trap surveys that were conducted annually during the dry season from 2003 to 2012 (see Johnson et al. 2006 for details). Camera traps were set along game trails (Johnson et al. 2016), and we assumed photographs of each felid species accurately represented their respective activity patterns. Each photograph was classified as a notionally independent event following O’Brien et al. (2003). Statistical modeling of activity patterns was carried out using circular statistics (Zar 1996). We constructed models predicting daily activity as a function of continuous trigonometric predictor variables, describing one ($cos\Theta$, $sin\Theta$) and two ($cos2\Theta$, $sin2\Theta$) complete cycles in a 24-hour period with $\Theta = \pi t/24$, where t is time in hours (Ross et al. 2013). We first tested whether activity cycles differed among species using a categorical predictor with levels indicating species. If a significant difference occurred, then we determined whether each species was diurnal, nocturnal, or crepuscular. To examine difference in activity pattern between the felid species, a kernel density method was implemented (Ridout and Linkie 2009). Non-parametric kernel density functions were fitted using the diel activity data of each species in the package overlap_0.3.0 in R (Ridout and Linkie 2009; Linkie and Ridout 2011; Meredith and Ridout 2014). The non-parametric estimator Δ_4 (coefficient value of overlap) was reported for this study due to its superiority for sample sizes that are greater than 50 (Schmid and Schmidt 2006; Ridout and Linkie 2009; Meredith and Ridout 2014).

To investigate if the two felid species partitioned habitats, we used elevation differences of each species' records as a proxy for habitat differences. We could not determine differences in habitat use directly because our entire study site was covered in closed canopy forests, and GIS or satellite data was not available to discern the subtle differences in tree species and vegetation types. Our study site was hilly with relatively steep slopes (Johnson et al. 2009), and elevation had a strong influence on vegetative communities (Davidson 1998). In addition, previous research showed that elevation can affect resource partitioning among carnivores owing to the habitat and other resource differences along elevational gradients (Tsunoda et al. 2017). We used all confirmed records of each species in our analysis, which included the elevation of each camera-trap photo and elevation of each DNA-confirmed scat. To test for differences in elevation, we used a multivariate regression model which treated elevation as a main predictor of the species presence/absence data.

RESULTS

We used 49 scats from Asian golden cats and 57 scats from leopard cats; all were confirmed by DNA analysis to be from those species. Other scats confirmed to species by DNA analysis during the main period of our study (February 2010 to March 2012) were: dhole (*n* = 194); tiger (*n* = 11); clouded leopard (*n* = 6); large Indian civet (*Viverra zibetha*; *n* = 11); crab-eating mongoose (*Herpestes urva*; *n* = 3); macaque (*Macaca* spp.; *n* = 1); and domestic dog (*Canis lupus familiaris*; *n* = 1). Mean (± SD) scat diameter was significantly larger ($t_{85} = -5.13$, $P < 0.001$) for Asian golden cats (2.1 ± 0.3 cm; range = 1.5 – 3.0 cm) than leopard cats (1.8 ± 0.2

cm; range = 1.3 – 2.3 cm). The range of scat diameters of both felids overlapped the range of scat diameters for dhole (1.2 – 4.0 cm), clouded leopard (1.5 – 2.5 cm), large Indian civet (2.3 – 4.0 cm), and crab-eating mongoose (1.7 – 1.9 cm). Most scats of Asian golden cats were found singly (76.0%); the remainder were found in latrines of 2 or 3 scats. Similarly, most scats of leopard cats were found singly (73.8%); the remainder were found in latrines of 2 – 4 scats. Only one latrine contained scats of both Asian golden cats and leopard cats (2 scats from each species).

For Asian golden cats, there were remains of at least 13 species in the scats, including 4 ungulate species (Table 2). Ungulates comprised 35.3% of all biomass consumed, followed by murids (23.1%), and other carnivores (14.8%; Table 2). For leopard cats, there were remains of at least 8 species in the scats (Table 2). Murids (79.1% of biomass consumed) were the most consumed category in the leopard cat diet, followed by birds (6.9%), squirrels (4.5%), and treeshrews (4.0%; Table 2). There was a significant difference in the overall diet between species ($X^2 = 38.44$, $P < 0.001$). The individual prey categories that significantly differed between species were ungulates ($P < 0.001$), carnivores ($P = 0.017$), and murids ($P < 0.001$). Niche breadth (B) was nearly twice as high for Asian golden cats (8.44) as for leopard cats (4.54; Table 2), and dietary overlap (R_0) between species was 0.60.

The percentage of ungulate biomass available in NEPL was 68% wild pig, 19% sambar, 8% muntjac, and 5% serow. The biomass of ungulates consumed by Asian golden cats did not reflect the biomass available, as they showed a strong selection for muntjac ($D = 0.91$), whereas serow ($D = -0.18$), wild pig ($D = -0.65$), and sambar ($D = -1.00$) were avoided (Fig. 2).

We obtained 93 independent photos of Asian golden cats and 156 independent photos of leopard cats during the study. The activity patterns significantly differed between species ($F_{1,38} =$

36.43, $P < 0.001$) because the Asian golden cat was mostly diurnal, whereas the leopard cat was mostly nocturnal (Table 3). The overall overlap in activity between the two species was moderate (0.52 Δ_4), because both species were partly active both day and night (Fig. 3). The highest degree of overlap occurring during nocturnal hours (Fig. 3). There was no significant difference ($F_{1,351} = 1.54$, $P = 0.220$) in elevation between the two felid species.

DISCUSSION

Diets differed between Asian golden cats and leopard cats, primarily because of greater consumption of ungulates and carnivores by Asian golden cats, and greater consumption of murids by leopard cats. Consequently, the dietary overlap between the felid species was relatively low, which did not support our prediction that they should have high dietary overlap. Also contrary to our prediction, ungulates comprised 35% of the diet of Asian golden cats, which was more than small mammals (33% for murids, squirrels, and treeshrews, combined). Overall, muntjac were the most consumed prey species of Asian golden cats; thus our results differed from previous studies with lower sample sizes that showed small rodents, birds, and reptiles, were the most common prey items of this species (Lim 2002; Kawanishi and Sunquist 2008; Xiong et al. 2017). Overall, body size appeared to influence prey selection of Asian golden cats, as the muntjac (20-28 kg; Francis 2008), was selectively consumed over medium-sized ungulates, whereas the largest ungulate was not consumed at all (Fig. 2). We therefore conclude that consumption of ungulates by Asian golden cats is primarily due to predation, rather than scavenging. If ungulates had been scavenged, then consumption would have been similar to available biomass, assuming that ungulate species had similar rates of natural mortality. Instead, there was a strong selection for muntjac regardless of ungulate densities, probably because this species was the smallest ungulate available to Asian golden cats. In addition, if ungulate carcasses had been available in our study site, leopard cats presumably would have scavenged as well, yet only a fraction of one scat from leopard cats contained muntjac. Furthermore, Asian golden cats likely did not scavenge from kills of large carnivores, because concurrent dietary studies in NEPL showed that dholes preyed most on muntjac and sambar (Kamler et al. 2012a, In Press) whereas tigers preyed most on wild pig and sambar (Vongkhamheng 2011); yet sambar was not detected in scats of Asian golden cats. The lack of consumption of sambar by Asian golden cats was probably because the large body size of sambar (180-260 kg; Francis 2008) made it less vulnerable to predation by a mesofelid.

A major limitation of our study is that we could not determine if Asian golden cats were feeding on adult or young ungulates. We assumed that Asian golden cats consumed ungulates that weighed on average 24 kg, which represents adult muntjac and the young of wild pig and serow. A 24-kg ungulate is 78% larger than the mean weight of Asian golden cats, but only 50% larger than a large male Asian golden cat. Other solitary felids prey on, and often prefer, species that are more than twice their average body size, including leopards (Rostro-García et al. 2018), cheetahs (Rostro-García et al. 2015), tigers (Hayward et al. 2012), and snow leopards (*Panthera uncia*; Lyngdoh et al. 2014). Thus, it is likely that Asian golden cats, particularly males, were capable of regularly preying on adult muntjac and young of larger ungulate species.

Smaller carnivores, primarily civets, also were an important part of the diet of Asian golden cats. Consumption of a common palm civet by Asian golden cats was recorded in Malaysia (Lim 2002), and remains of short-tailed weasel (*Mustela erminea*) was detected in 2 of 10 scats from Asian golden cats in China (Xiong et al. 2017), indicating small carnivores might be important prey of Asian cats throughout their distribution. Consumption of small carnivores by Asian golden cats in NEPL was likely due to predation instead of scavenging, because no small carnivores were detected in the scats of leopard cats, indicating carcasses of small carnivores were not readily available on our study site. The relatively high consumption of civets by Asian golden cats in our study could have been due to intraguild predation, which occurs when a larger carnivore preys on smaller carnivores not only for food, but also to reduce competition for shared resources (Polis et al. 1989; Kamler et al. 2012b). Because small mammals are consumed both by Asian golden cats and civets (Francis 2008), Asian golden cats theoretically could have benefited from reduced competition for this shared resource by preying on civets.

In addition to ungulates and small carnivores, murids were an important part of the diet of Asian golden cats (23% of biomass consumed), although less important than reported in previous studies (Kawanishi and Sunquist 2008; Xiong et al. 2017). Overall, Asian golden cats consumed larger rodents (i.e., brush-tailed porcupines, rats, and squirrels) more than mice or shrews (Table 2), although lack of data on densities prevented us from determining dietary selection among small mammals. Asian golden cats consuming larger rodents more than mice or shrews is consistent with an optimal foraging strategy, because the profitability of prey species for carnivores increases rapidly with prey body size, as long as there is little or no increase in handling cost (MacCracken and Hansen 1987). Thus, it likely is more energetically efficient for Asian golden cats to consume larger rodents compared to mice and shrews.

It is noteworthy that domestic goat was detected in one scat from an Asian golden cat, because goats are not common in the core zone of NEPL (Lim 2017). There are 34 villages in the management zone and edge of the core zone in NEPL, and most villagers raise large livestock (domestic water buffalo and cattle) which is their principal source of cash income, whereas only

15-20% of villagers raise goats (Lim 2017). Nonetheless, between 2007 and 2012 local villagers in NEPL reported that Asian golden cats caused some small livestock losses (Lim 2017), indicating that conflicts between local people and Asian golden cats did occur. There are two reports of Asian golden cats killing livestock calves in Myanmar (Gee 1961), suggesting predation on livestock occurs in other areas of their distribution.

Compared to other felids, Asian golden cats exhibit extreme sexual dimorphism in body size, with adult males (12-16 kg) typically 50-75% larger than adult females (8-10 kg; Grassman et al. 2005a; Reichler 2018; Sunquist and Sunquist 2002), which might lead to inter-sexual differences in diet. For example, other solitary felids, including leopards and cheetahs (*Acinonyx jubatus*), exhibit sexual dimorphism in body size, which results in males preying on substantially larger prey than females (Rostro-García et al. 2015, 2018). Male Asian golden cats therefore might prey on substantially larger species than females, which could be investigated by determining the sex of scat samples (Rostro-García et al. 2018). Although it was beyond the scope of our study, we recommend that future research determine the inter-sexual differences in diet of Asian golden cats, given the extreme sexual dimorphism exhibited by this species.

Murids dominated the diets of leopard cats (79% biomass consumed), which is consistent with the findings of previous studies (Table 1), suggesting leopard cats are a murid specialist throughout their distribution. Overall, mice were the most common prey item of leopard cats, and biomass consumed of mice was almost 8 times higher for leopard cats than Asian golden cats. In contrast to Asian golden cats, the diet of leopard cats did not include any mammal species > 0.5 kg, with two exceptions: muntjac and brush-tailed porcupine each comprised a fraction of one scat, suggesting they represented scavenged remains (Klare et al. 2014). The diet of leopard cats in NEPL appeared less diverse compared to previous studies (Table 1), because we did not detect small reptiles or insects in their diet. The low diversity of prey species was reflected in a relatively low niche breadth estimate for leopard cats, which was almost half that of the Asian golden cat (Table 2). The differences in niche breadth values were likely related to body size differences, because the larger Asian golden cats had access to larger and more diverse prey species compared to leopard cats.

The mean scat diameters in this study are the same as that reported for DNA-confirmed scats of Asian golden cats and leopard cats in Malaysia (2.1 and 1.8 cm, respectively; Kawanishi and Sunquist 2008), indicating scat size of each species likely are similar across their distributions. The size of leopard cat scats in our study raises concerns because several previous dietary studies only classified scats as leopard cats if they were 1 cm, or 1.0-1.5 cm, in diameter (Table 1). In our study, none of the leopard cat scats were as small as 1 cm, and 87% of leopard cat scats were > 1.5 cm, indicating several previous dietary studies might have excluded large numbers of potential leopard cat scats. In addition, the scat diameters of crab-eating mongoose fell completely within the range of both felid species, and the scat diameters of all other small sympatric carnivores partially overlapped both felid species. This indicates that previous dietary studies of leopard cats might inadvertently have included scats from other sympatric small carnivores, particularly given how common it is for field researchers to misidentify carnivore scats (Baines et al. 2013; Janečka et al. 2008; Weiskopf et al. 2016), including leopard cat scats (Karmacharya et al. 2016; Khatoon et al. 2019). Consequently, we recommend that genetic analyses be used in all future studies that investigate the diets of small felids and other sympatric carnivores based on scat collections.

The activity patterns differed between Asian golden cats and leopard cats, which supported our prediction that they should exhibit temporal partitioning. Leopard cats were nocturnal whereas Asian golden cats were diurnal in NEPL, which was consistent with several studies that reported activity patterns of these two species (Grassman et al. 2005a, b; Johnson et al. 2009; Lynam et al. 2013; McCarthy et al. 2015b; Mukherjee et al. 2019), indicating their activity patterns are relatively consistent across their distributions. More recent camera-trap surveys in NEPL showed that the activity of Asian golden cats overlapped most strongly with muntjac, sciurids, and birds, indicating the activity patterns of this felid was driven by prey (Rasphone et al. In Press). Similarly, the activity of leopard cats overlapped most strongly with murids, indicating the activity patterns of this felid also were driven by its main prey, rather than avoidance of Asian golden cats (Rasphone et al. In Press). Overall, it appears that hunting different prey likely facilitated different activity patterns between the felid species, which presumably would have reduced encounter rates between them and ultimately reduced the potential for interference competition.

The two felid species did not significantly differ in their use of elevation, which did not support our prediction that they should exhibit elevational partitioning. This result suggests that the two felid species did not exhibit habitat partitioning at a large scale. Similarly, occupancy models developed from more recent camera-trap surveys in NEPL showed that the two felid species had high (97%) positive associations with each other (Rasphone 2018), indicating leopard cats were not spatially avoiding Asian golden cats at large scales. Our results are consistent with the niche complementarity hypothesis, with states that a high degree of overlap in 1 or more niche components (i.e., habitat and space) should be associated with a low degree of overlap in 1 or more other niche component (i.e., diet and time; Schoener 1974; Lucherini et al. 2009). Nonetheless, leopard cats may have avoided Asian golden cats at smaller scales not investigated in this study, such as the level of the home range, feeding site, or resting site

(Rostro-García et al. 2015). Given the resources measured in this study, we conclude that leopard cats coexist with Asian golden cats primarily by exhibiting dietary and temporal partitioning.

During our study, Asian golden cats and leopard cats were sympatric with three other felids: tigers, clouded leopards, and marbled cats. Although diets of clouded leopards and marbled cats were unknown, a concurrent study on DNA-confirmed tiger scats showed that this species consumed mostly wild pig (50%), sambar (15%), and bear (15%; Vongkhamheng 2011). This indicates that the food niche overlap between tigers and Asian golden cats and leopard cats is minimal. In addition, the tiger population in NEPL consisted of just a few individuals, which have become extirpated (Rasphone et al. 2019), suggesting the tiger population had minimal impacts on the behaviors or niches of Asian golden cats and leopard cats. Clouded leopards and marbled cats both are semi-arboreal and have relatively low densities in NEPL (Rasphone 2018), suggesting they have different niches and likely minimal impacts on the behaviors of the terrestrial Asian golden cats and leopard cats. Nonetheless, given that Southeast Asia contains the highest diversity of felids in the world (Luo et al. 2014), we recommend that future research in the region investigate the trophic niche overlaps of the entire felid community, as that will help us understand the complete suite of mechanisms that allows such a diverse community of felids to partition resources and coexist.

Overall, our results indicate that Asian golden cats are generalists and opportunistic foragers with a high niche breadth. This species has a remarkably diverse diet with prey ranging in size from mice and civets to wild pigs and serow. Nevertheless, there was high consumption and strong selection for muntjac by Asian golden cats, indicating this ungulate likely is important for maintaining populations of Asian golden cats. Consequently, conservation efforts for Asian golden cats in the remaining parts of their distribution should consider the management of muntjac populations, particularly in areas where mouse deer are absent. In Southeast Asia, Asian golden cats, along with muntjac and other prey species, are facing steep declines because of the snaring crises in the region (McCarthy et al. 2015a; Gray et al. 2017); we therefore recommend that managers monitor populations both of Asian golden cats and muntjac. If Asian golden cat and muntjac populations are low or declining, then law enforcement activities, such as snare removal and number of patrols, should increase to help stabilize and improve numbers of this mesofelid and its main prey.

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Table 1.−Summary of dietary studies of leopard cats, excluding those from Japanese islands, with sample sizes > 20 scats. The DNA indicates if genetic analysis was used on scats to confirm species. For non-DNA studies, the diameter used to classify scats as leopard cats is given (NA = not available).

Country – Site	Sample size	DNA	Scat diameter used	Top three prey categories
Bangladesh				
Sundarbans East WS[1]	21	No	NA	Murid (52%), insect (29%), bird (24%)
China				
Laohegou NR[2]	93	Yes	----	Rodent (~90%), ochotonid (~77%), small carnivore (~30%)
India				
Khangchendzonga BR[3]	37	No	1-1.5 cm	Rodent (89%), ochotonid (22%), bird (11%)
Laos				
Nam Et-Phou Louey NPA[4]	57	Yes	----	Murid (79%), bird (7%), sciurid (5%)
Malaysia (Borneo)				
Tabin WR and plantations[5]	72	No	1 cm	Murid (90%), herpetofauna (20%), insects (11%)

Pakistan				
Ayubia NP[6]	22	Yes	----	Rodent (91%), bird (46%), herpetofauna (27%)
Philippines				
Negros Occidental farm[7]	25	No	NA	Rodent (96%), bird (8%)
Negros Occidental farm[8]	51	No	1-1.5 cm	Rodent (96%), herpetofauna (20%), bird (12%)
Singapore				
Pulau Tekong island[9]	65	Yes	----	Murid (100%), insect (52%), herpetofauna (20%)
South Korea				
Country wide[10]	280	No	1-1.5 cm	Rodent (90%), bird (14%), insect (5%), herpetofauna (5%)
Thailand				
Huai Kha Khaeng WS[11]	52	No	1 cm	Murid (~65%), herpetofauna (~15%), sciurid (~13%)
Kaeng Krachan NP[12]	25	No	NA	Murid (36%), herpetofauna (20%), leporid (8%), tupaiid (8%)
Phu Khieo WS[13]	53	No	1-1.5 cm	Murid (85%), insect (21%), sciurid (4%), bird (4%), tupaiid (4%)

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[1] Khan 2004; [2] Xiong et al. 2017; [3] Bashir et al. 2014; [4] This study; [5] Rajaratnam et al. 2007; [6] Shehzad et al. 2012; [7] Fernandez and de Guia 2011; [8] Lorica and Heaney 2013; [9] Chua et al. 2016; [10] Lee et al. 2014; [11] Rabinowitz 1990; [12] Grassman 2000; [13] Grassman et al. 2005b

Table 2.−Diet composition expressed as percentage of ingested biomass calculated using the model from Chakrabarti et al. (2016; B-C), percentage of ingested biomass calculated using the model from Baker et al. (1993; B-B), percentage of scat volume (Vol), frequency of occurrence per scat (Occ), and dietary niche breadth (*B*) of Asian golden cats (*Catopuma temminckii*) and leopard cats (*Prionailurus bengalensis*) in Nam Et-Phou Louey National Protected Area, Laos.

	Asian golden cat (*n* = 49 scats)				Leopard cat (*n* = 57 scats)			
Prey category	B-C	B-B	Vol	Occ	B-C	B-B	Vol	Occ
Rodent	40.3	44.3	57.7	71.4	85.3	91.0	88.8	93.0
Brush-tailed porcupine (*Atherurus macrourus*)	12.1	8.5	8.6	10.2	1.7	0.3	0.6	1.8
Squirrel (Sciuridae)	5.1	7.0	8.0	12.2	4.5	6.6	3.5	7.0
Muridae	23.1	28.8	41.1	55.1	79.1	84.2	84.7	91.2
Rat size	5.6	6.0	9.4	14.3	27.6	29.4	25.0	28.1
Mouse size	3.8	5.1	7.2	12.2	28.8	36.3	35.9	43.9
Unknown size	13.7	17.7	24.5	28.6	22.7	18.5	23.7	24.6
Treeshrew (Tupaiidae)	5.2	7.7	8.9	14.3	4.0	2.1	3.6	5.3
Shrew (Soricidae)	2.1	3.3	4.1	6.1	1.8	0.9	2.5	3.5
Ungulate	35.3	25.3	17.1	20.4	2.0	1.3	0.7	1.8
Muntjac (*Muntiacus* spp.)	22.3	17.2	10.8	12.2	2.0	1.3	0.7	1.8
Wild pig (*Sus scrofa*)	10.5	6.9	5.1	8.2	0.0	0.0	0.0	0.0
Mainland serow (*Capricornis sumatraensis*)	1.3	0.6	0.6	2.0	0.0	0.0	0.0	0.0
Domestic goat (*Capra aegagrus hircus*)	1.3	0.6	0.6	2.0	0.0	0.0	0.0	0.0
Carnivore	14.8	17.0	9.0	10.2	0.0	0.0	0.0	0.0
Palm civet[a]	10.7	15.7	6.9	8.2	0.0	0.0	0.0	0.0
Hog badger (*Arctonyx collaris*)	4.1	1.3	2.0	2.0	0.0	0.0	0.0	0.0
Birds	2.3	2.5	3.2	8.2	6.9	4.7	4.4	5.3
Niche Breadth *B*	8.44				4.54			

[a] Common palm civet (*Paradoxurus hermaphroditus*) or masked palm civet (*Paguma larvata*).

Table 3.−Estimates of coefficients (± SE) of diel activity models and best models with adjusted R2 values for Asian golden cats (AGC) and leopard cats (LC) photographed in camera traps in Nam Et-Phou Louey National Protected Area, Laos. For CosΘ, a species is determined to be nocturnal with a positive coefficient, or diurnal with a negative coefficient. Significant values ($P < 0.05$) are marked with *.

	SinΘ	**CosΘ**	**Sin2Θ**	**Cos2Θ**	**Best Model**	**Adjusted R^2**
AGC	-0.008 ± 0.007	-0.014 ± 0.007*	-0.0006 ± 0.007	0.001 ± 0.007	CosΘ	0.127
LC	0.002 ± 0.004	0.042 ± 0.006*	0.005 ± 0.006	0.008 ± 0.006	CosΘ	0.702

Figure legends

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

Fig. 2.—Jacobs' (1974) electivity index (*D*) of ungulates based on percent biomass consumed by Asian golden cats in the Nam Et-Phou Louey National Protected Area, Laos. Body mass of adult female ungulates are given, taken as the lower range of body mass reported by Francis (2008).

Fig. 3.—Activity patterns and overlap of Asian golden cats and leopard cats in the Nam Et-Phou Louey National Protected Area, Laos. Activity patterns were based on the time of independent camera-trap photographs, and they were significantly different ($P < 0.001$) between species. The coefficient of temporal overlap between the species (gray shading) was 0.52 (95% CI = 0.38-0.59). Dawn and dusk represent 30 minutes before and after sunrise and sunset, respectively.