The intraguild interactions of large carnivores and their impacts on their prey and other smaller carnivores in the Nam Et - Phou Louey National Protected Area, Lao PDR



A thesis submitted for the degree of

Doctor of Philosophy

Michaelmas Term 2018

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Abstract

In an environment, the species populations are not only affected by the abiotic factors but also by the interactions between the organisms. In contexts where human-induced habitat loss and anthropogenic disturbances are prominent, inter-specific interaction will undoubtedly increase, at least initially, as wild animals are confined to smaller areas with greater resource limitations. In light of this, a key question of conservation concern emerges: what mechanisms do subordinate predators adopt in order to persist alongside dominant predators when space and prey resources are limited? This thesis, therefore, aimed to investigate interactions of sympatric carnivores (felids and dhole) in the Nam Et - Phou Louey National Protected Area (hereafter NEPL) in northern Lao PDR. The NEPL harbours six felid species (tiger *Panther tigris*, leopard *Panthera pardus*, clouded leopard *Neofelis nebulosa*, Asian golden cat *Catopuma temminckii*, marbled cat *Pardofelis marmorata*, and leopard cat *Prionailurus bengalensis*) and dhole *Cuon alpinus*. Over the past decade, the main threat to the flora and fauna of the NEPL has been the unregulated over-harvesting of animals and plants and forest clearance. This study not only will contribute to our scientific knowledge of NEPL's carnivore species, the findings will also benefit conservation efforts via providing much-needed information regarding their ecology and status to guide decision making. First, I investigated the status of all hypercarnivores and prey species of NEPL (Chapter 2). My results showed that tiger and leopard had been extirpated, most likely due to the rise of indiscriminate snaring. Consequently, clouded leopard and dhole, the largest and most common remaining hypercarnivores. Large ungulate prey species (e.g., gaur *Bos gaurus* and sambar *Cervus unicolor*) were rare, whereas smaller ungulate species were relatively common. Overall, NEPL still had rich communities of carnivores and prey. Second, I estimated density trends of clouded leopard, leopard cat, and marbled cat, to better understand what likely happens to smaller felids when the top felid, tiger, disappears from the system (Chapter 3). The findings showed a declining trend in density across the study years for all three felid species, with a stronger rate of decline for clouded leopard and leopard cat. Snaring likely was responsible for the continuing decline of the smaller felids, and this factor was likely to override any potential effects of mesopredator release on their densities and interactions. Third, I assessed spatial and temporal niche segregation, to understand factors facilitating coexistence of all sympatric hypercarnivores (Chapter 4). Dhole and clouded leopard did not have high spatial and temporal avoidance, but presumably had some differences in dietary niches. Asian golden cat adopted a cathemeral activity pattern and is likely to have diet specialisation to co-occur with dhole and clouded leopard. The leopard cat and marbled cat are likely to coexist with the Asian golden cat via prey specialisation whereas leopard cat and marbled cat clearly segregated temporally and potentially by diet. Fourth, I predicted the distribution of suitable habitat across the country for the three largest remaining hypercarnivores: dhole, clouded leopard, and Asian golden cat (Chapter 5). My results highlighted the importance of the National Protection Forest Areas for the conservation of carnivores in the country, especially in the northern provinces and along the central Annamite landscape. Overall, my findings contributed to the knowledge of the ecology and interactions of a diverse carnivore community in northern Laos, and results will be used to guide management plans and conservation efforts for carnivores and their prey within NEPL and other landscapes throughout the country.

Acknowledgements

This journey has taught me so much. I am very grateful to have been on this road and I could not have arrived at my destination without a number of people who aided me in various ways. I would like to express my deep gratitude to my supervisor Prof David Macdonald for believing in me and giving me this great opportunity.

The research was supported by a grant to DWM from the Robertson Foundation and National Geographic Society, for which I am deeply grateful.

I would like to offer my special thanks to the Wildlife Conservation Society, Laos, and the Nam Et - Phou Louey National Protected Area for their extensive in-kind support and for their efforts towards planning and implementing the research.

I cannot shower enough thanks on Mr. Phonesouk Chanthalavong for his excellent assistance in field work preparation and implementation, and data management, and Jan F. Kamler for being such a great teacher and friend, guiding and supporting me through the large chunk of this journey. I am grateful to Marc Kéry and Zaneta Kaszta for their help on statistical modelling processes.

I would like to extend my thanks to all the members of my survey team, Orn, Senjaolo, Maihiem, Bouakham, Anonh for their dedication and hard work in the field, they are the backbone of this study, and together they made the best field team.

I am particularly grateful for the assistance given by Mike Meredith, Ngumbang Juat and Dr. Lucy Tallents. Thank you Aphone Viengkhamhak and Jay White for always taking their time to help me whenever I requested for datasets.

Thank you to my WildCRU family for your friendship and support over the years. Thank you Joanna Ross, Amy Hinks and Rosie Salazar for always being so helpful and for always making

our Red Panda Office a great environment and welcoming place during my early DPhil years. Thank you Jennifer Spencer for friendship and support.

Thank you Andrea de Marinis for always being there for me when I needed a small talk, a company to the Bodleian Library, and a coffee-mate. Thank you Cedric Tan for support, friendship and for always being my great, fun Asian sibling here in the foreign land. Thank you Moreangels Mbizah, Greta Semplici, Vania Pinto, Naomi Creutzfeldt, Leandro Abade, Tass and Titi for friendship and support. I am extremely grateful to have you in my life. Thank you Colin Moore for your patience, love and support. No words can describe how grateful I am to have you in my life. This journey would have been much harder without you.

Finally, I wish to thank my big family for their love, support and encouragement throughout my study. Thank you Dolamanh Rasphone and Kiaosamphanh Rasphone and Khounsasanh Rasphone for being such super great siblings. You are always there whenever I call for help.

I dedicate this work to my parents. Your love and support have made me who I am today. I can never thank you enough. You have fought so hard to bring me and my siblings up. This work shows that your efforts did not go to waste. The memories of me accompanying mom in the kitchen at 5am while she was preparing sticky rice and teaching me little things every day during my primary school years are the fondest memories in my life, they put a smile on my face when I think of them. I always remember once mom told me to always do my best to pursue my dreams in education and if it did not work out even then, I can always go back home to sell grilled chicken. These words have given me strength to fight without fear of failure and I am forever thankful for them.

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Chapter 1

General Introduction

Preface

Carnivores are fundamentally important in maintaining healthy and balanced ecosystems (Estes *et al.* 2011). They play a pivotal role in regulating prey populations and their presence contributes to overall biodiversity values (Steneck 2005). Fear of predation by carnivores is known to influence spatial distribution, habitat selection and vigilance behaviour of their prey (Macdonald *et al.* 2013). Loss of or decline in populations of hypercarnivores (e.g., felids and dhole) and mesocarnivores (e.g., viverrids and mustelids) can alter prey population densities and distributions, which in turn can affect habitat composition within an environment (Ripple and Beschta 2006). Previous research has shown the negative consequences which can follow the removal or decline of carnivore populations (Terborgh *et al.* 2001; Sinclair *et al.* 2003; Smith *et al.* 2003; Ripple and Beschta 2006; 2007). The primary threats to most carnivores include habitat loss (Sunarto *et al.* 2013), the depletion of prey populations (Henschel *et al.* 2011), human-carnivore conflict, hunting for consumption and for trade (Sharma *et al.* 2014), and infectious disease (Hunter *et al.*, 2011; Macdonald *et al.*, 2013). In addition to their ecological importance, large carnivores are rare (Hunter *et al.*, 2011) and many populations are severely threatened (Wilting *et al.*, 2006), which makes their conservation of paramount importance for conserving biodiversity as well as for maintaining ecological integrity within systems. Effective conservation of large carnivores requires an in-depth understanding of their ecology. Such an understanding will help us to understand better how human-induced changes affect carnivore populations, and how best to mitigate such human impacts.

One of the key challenges in carnivore ecology is understanding the interactions between members of a guild. This is particularly important as intraguild interactions are one of the main factors influencing population dynamics (Holt and Polis 1997b). In order for different species that share common resources to coexist in a landscape, they must have different ecological traits or niches. The main aim of this project therefore is to investigate the mechanisms of co-existence within the carnivore communities of the Nam Et - Phou Louey National Protected

Area (hereafter NEPL), a relatively well protected area in northern Laos that has an especially high diversity of carnivore species.

Intraguild Interactions

In an environment, the species populations are not only affected by the abiotic factors but also by the interactions between the organisms (Meserve *et al.* 1999). Competition is one form of interaction where species attempt to use the same limited resources (such as food or living space) and which can occur both within and between species (Begon *et al.* 1996). Competition between members of different species is known as interspecific competition which consist of two types – exploitation and interference (Schoener 1983; Reece *et al.* 2014). Exploitation is an indirect interaction between competing species of the same guild via a shared resource (Schoener 1983). For instance, individuals of one species can be more efficient in using the common resources which in return can deplete availability of the resources for the other sympatric species. For interference competition, members of one species directly interact with members of other species through a display of aggressive behaviors such as killing, harassing or predating (Schoener 1983; Polis and Holt 1992). A mixture of competition and predation is known as intraguild predation or IGP (Holt and Polis 1997a).

Intraguild predation is a type of interaction where top predators kill and consume or harass their potential competitors (Holt and Polis 1997a). This typically occurs where at least two members of the same guild compete for the same limited resources (Linnell and Strand 2000) and IGP can shape the structuring of species communities in an ecosystem (Heithaus 2001). For example, intermediate predators will avoid optimal habitat where risk of predation by top predators is high, as shown with leopard *Panthera pardus* and tiger *Panthera tigris* in the Royal Chitwan National Park, Nepal (Seidensticker et al., 1990). Therefore, IGP can cause the exclusion of subordinate predators from a given community by influencing behaviour,

distribution, and densities (Dill *et al.* 2003; Macdonald *et al.* 2010a). While removal of subordinate predators lowers predation pressure on shared prey species, it can also contribute to the effects of trophic cascades by providing redundancy in predation (Finke and Denno 2005). For instance, in an ecosystem where one top predator species is removed, the remaining predators may continue to prey on the same prey species without necessarily expanding their dietary breadth to cover the prey species of the removed top predator. In contexts where human induced habitat loss and anthropogenic disturbances are prominent, IGP will undoubtedly increase, at least initially, as wild animals are confined to smaller areas with greater resource limitations. In light of this, a key question of conservation concern emerges: what mechanisms do subordinate predators adopt in order to persist alongside dominant predators when space and prey resources are limited?

Coexistence – Niche Segregation

Understanding how similar species within ecological communities coexist is a key question in ecology as we are seeking to explain what factors affect their occurrence (Wiens 1977; Gordon 2000; Gravel *et al.* 2011). Existing research has shown that resource partitioning can promote coexistence (Macarthur and Levins 1967; Roughgarden 1974). In diverse carnivore guilds, it is apparent that competing species partition resources through niche differentiation or niche segregation (i.e., different physical traits and behavioural/biological traits) to coexist in the same region (Johnsingh 1992; Karanth and Sunquist 1995; Venkataraman 1995). Niche differentiation may involve segregation in the species' use of habitat, food or time (Schoener 1974; Fedriani *et al.* 2000; Kronfeld-Schor and Dayan 2003; Sinclair *et al.* 2003; Azlan and Sharma 2006; Balme *et al.* 2007; Rajaratnam *et al.* 2007a; Lucherini *et al.* 2009; Lynam *et al.* 2013; Ross *et al.* 2013). Niche separation is driven by competition (Dayan *et al.* 1992) and through that separation, the frequency of potentially negative encounters between subordinate

and dominant species is minimised (Durant 1998; Fedriani *et al.* 2000; Linnell and Strand 2000; Creel 2001) and, hence, species can coexist.

Carnivores of Nam Et - Phou Louey

The NEPL in northern Lao People's Democratic Republic (Lao PDR), or Laos, contains a particularly outstanding diversity of carnivores, and is a refuge for the last known population of tigers in Indochina (Johnson *et al.*, 2009). The NEPL harbours six felid species (tiger, leopard, clouded leopard *Neofelis nebulosa*, Asian golden cat *Catopuma temminckii*, marbled cat *Pardofelis marmorata* and leopard cat *Prionailurus bengalensis*), dhole *Cuon alpinus*, two bear species (Asiatic black bear *Ursus thibetanus* and sun bear *Helarctos malayanus*). The NEPL also lies within the second most important core area in the world for supporting small carnivore taxa of conservation concern which includes at least 11 smaller carnivore species from the civet, weasel and mongoose families (large Indian civet *Viverra zibetha*, small Indian civet *Viverricula indica*, spotted linsang *Prionodon pardicolor*, masked palm civet *Paguma larvata*, common palm civet *Paradoxurus hermaphroditus*, Owston's civet *Chrotogale owstoni*, striped-back weasel *Mustela strigidorsa*, yellow-throated marten *Martes flavigula*, hog badger *Arctonyx collaris*, oriental small-clawed otter *Aonyx cinereus*, and crab-eating mongoose *Herpestes urva*).

Building on earlier studies carried out in the NEPL in 2003 (Johnson *et al.* 2006b; Johnson *et al.* 2009; Kamler *et al.* 2012; Vongkhamheng *et al.* 2013), an intensive camera trap survey conducted between March – May 2013 by the Wildlife Conservation Research Unit (WildCRU) and the Wildlife Conservation Society Lao PDR Program has confirmed the persistence of a high diversity of felids and other carnivores within the site. The diversity of carnivores within this site means that the NEPL provides a particularly appropriate context in which to further investigate interactions within this guild. It is also the last remaining site in Indochina available

to investigate the effects of tiger on the entire carnivore community. Over the past decade, the main threat to the flora and fauna of the NEPL has been the unregulated over-harvesting of animals and plants, largely for illegal trade and to a lesser degree for subsistence (Johnson *et al.* 2009). Forest clearance, primarily for small-holder agriculture, has also had an important impact on the site (Johnson 2012). Recent studies estimate that the deforestation pressure on the NEPL has increased over the last ten years resulting in a deforestation rate of 0.57% between 2010 – 2013 which equivalents to 2,264 ha/year (Hansel *et al.* 2013). This loss also negatively impacts the habitat available for both carnivore and prey species. This study not only will contribute to our scientific knowledge of some of the NEPL's carnivore species (i.e., felids and dhole), the findings may also benefit their conservation via providing much needed information regarding their ecology and status to guide decision making and development of effective species conservation plan for the protected area as well as for the wider landscape within the country.

Study area description

Geomorphology

The NEPL is the largest national protected area (NPA) in Lao PDR, covering 596,864 ha of mountainous terrain across three provinces and nine districts including Luang Prabang Province (Viengkham, Phonxay and Phonthong Districts), Houaphan Province (Viengthong, Houamuang, Xamneua, and Aet Districts) and Xieng Khouang Province (Phoukoud and Kham Districts). Its northern boundary borders Vietnam. It is between latitude 19°50' - 20º50' N and longitude 103°00' - 103°53' E (Fig.1). The topography of NEPL is rugged, with elevation ranging from 400-2257 m, of which >60% is above 1000 m and 91% with slopes >12%.

Three major rivers drain the NEPL; the Nam Khan which flows through the centre of the park and forms in part the southern boundary, the Nam Nern to the southeast of the Phou Louey

Mountain; and the Nam Et draining the Phou Jae mountain in the north. The NPA is also defined by the high elevation Nam Ngao anthropogenic grasslands in the northwest and the Thamla fern-covered grasslands to the southeast. The climate in Lao PDR is tropical monsoonal with a rainy season lasting from May to October followed by a distinct dry season for the remainder of the year (Duckworth *et al.* 1999a). Annual rainfall ranges from 1400 to 1800 mm (Johnson 2012).

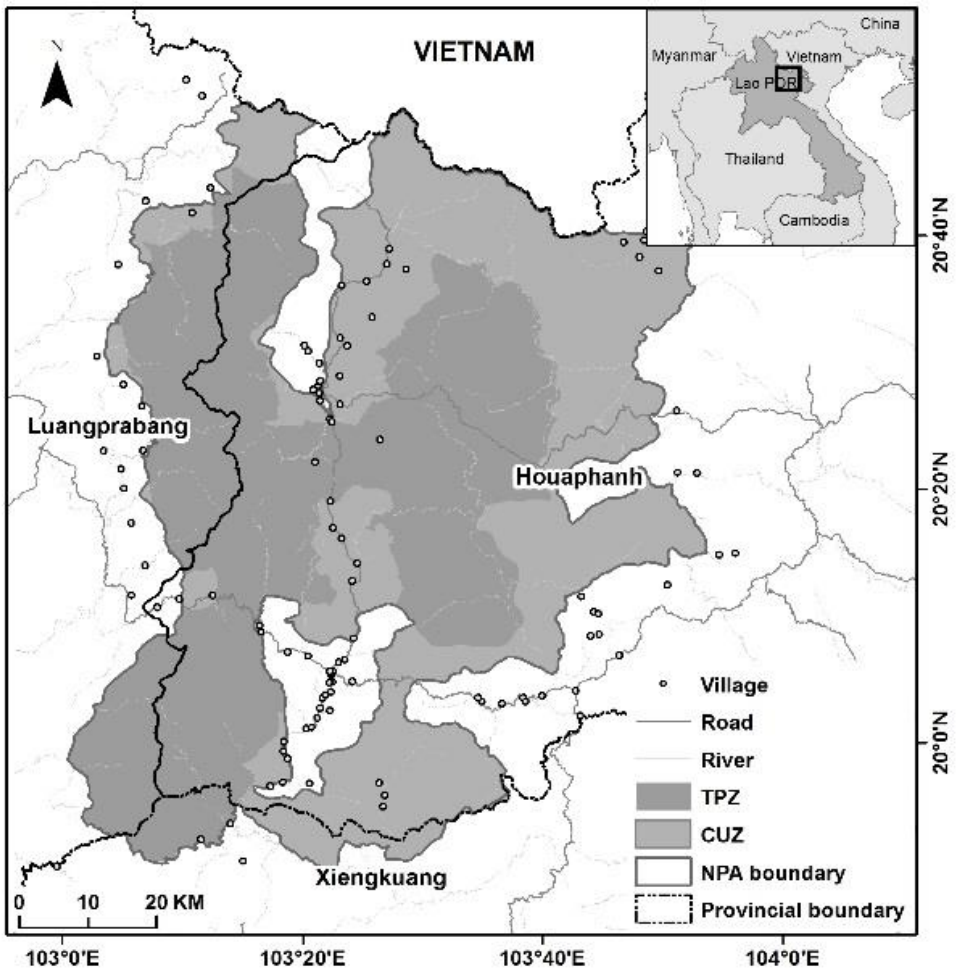


Fig. 1: Location map of Nam Et - Phou Louey National Projected Area

Habitat

The NEPL is characterized by mixed evergreen and deciduous forest with patches of anthropogenic grasslands, agricultural land and disturbed forests. Based on a 2013 land cover classification, 68% of the NEPL NPA is forest with a canopy cover of greater than 20%, of

which 6% was evergreen forest and the remaining 94% was semi-evergreen forest. A further 122,512 ha (24% of the total area) is classified as some form of degraded forest land (fallow or shrub) with a canopy cover of less than 20%.

Biodiversity

The NEPL ranks high in the national protected area system for contributing the highest biological diversity of any protected area in the Northern Highlands region of the country (Johnson *et al.* 2009). Apart from aforementioned carnivore species, the protected area contains six ungulate species (gaur *Bos gaurus*, sambar *Cervus unicolor*, Indochinese serow *Capricornis milneedwardsii*, small dark muntjac(s) *M. rooseveltorum* complex, northern red muntjac *Muntiacus vaginalis* and wild pig *Sus scrofa*), at least five species of primates, 299 bird species (where 17 species are Globally Threatened), more than 40 bat species, 30 reptile and amphibian species, and more than 314 plant species (Schreiber *et al.* 1989; Johnson 2012). Phou Louey Mountain is identified as especially important as it contains a distinctive montane bird community with ten species that are known from only one or two other localities in Laos. This level of species diversity makes the site of critical importance to biodiversity conservation (Johnson *et al.* 2009).

Socio-economic Status

Originally established in 1993 as two separate NPAs (the Nam Et - NPA and the Phou Louey NPA) with a combined area of 408,871 ha, these two areas were not actively managed until 2000 when the International Union for the Conservation of Nature (IUCN) first began to provide technical and financial support. This role was taken over by the Wildlife Conservation Society in 2003 who remains at the site to this day. Despite being two distinct NPAs, they have consistently been managed as a single unit. In 2007 district regulations establishing management and use guidelines recognized two extension areas to the NPA that at the local

level are considered an integral part of the NPA despite not being officially gazetted at the national level. These additional areas have been included in the analysis of this study, bringing the total NPA area to 596,864 ha.

Also, in 2007, the NPA was divided into a strictly protected core zone, known as the Totally Protected Zone (TPZ) where human access is prohibited, of 308,034 ha and a Controlled Use Zone (CUZ) – an area where sustainable use of natural resources for local livelihood is permitted – of 288,830 ha.

There are 34 villages inside the NPA management zone and 64 villages bordering the NPA boundary (Johnson, 2009). The population is ethnically diverse, comprising of three major ethno-linguistic groups including the Tai-Kadai (Tai Lao, Tai Dam, and Tai Deng), the Mon-Khmer (including Khm'u and Lao Khaa), and the Hmong-Mien (including Hmong, Hmu, and Lu Mien). Most families are engaged in subsistence activities with integration into the market economy developing rapidly. Rice is the staple food and is primarily produced through rotations of shifting cultivation on steep mountainous slopes while meat and vegetables are raised or harvested from the forest.

Research Aims

The overarching aim of this research is to investigate what different mechanisms are used amongst sympatric carnivore species to enable coexistence within the NEPL. There are 5 main species of focus, including an apex carnivore dhole, two meso-felids (clouded leopard, Asian golden cat) and two small felids (marbled cat and leopard cat). Although the body size of dhole overlaps those of clouded leopard and golden cat, dhole functions in large packs and can be considered apex predators, as they have the ability to kill large ungulates and other large carnivores, including tiger (Kamler *et al.* 2015). Population status and ecology of the five-

carnivore species of the NEPL, however, remains almost totally unknown in Laos. Due to the lack of leopard records since 2004 (Johnson *et al.* 2006b), the species is excluded from this study, The leopard may have already been extirpated as suggested by Rostro-García *et al.* (2016) and this study will further confirm the speculation. Although the preliminary survey in 2013 confirmed the presence of tiger in NEPL, the extremely low number of records suggested this species is on the blink of local extinction, which resulted in insufficient records for detailed investigation of interactions with other carnivores.

Dhole

The dhole or Asiatic wild dog *Cuon alpinus* is a highly social carnivore species, living in packs of about five to 25 adults (Durbin *et al.* 2004.). The population distribution range of dhole is currently limited to primarily South and Southeast Asia, but occurring at low density (Durbin *et al.* 2004.; Grassman *et al.* 2005b; Kamler *et al.* 2012). The species is classified as Endangered by the International Union for Conservation of Nature (IUCN - Kamler *et al.* 2015). The dhole (10 – 20 kg) is a habitat generalist and was reported to be found in various habitat types (including primary, secondary, mixed evergreen, semi-evergreen, grassland, shrub and degraded forests) at the elevation range from sea level up to 5,300m (Gray and Phan 2011; Aryal *et al.* 2015; Kamler *et al.* 2015). Previous dietary studies of dhole suggested that they prefer ungulate prey 40-60kg and if such prey size is not available, they will selectively prey on smaller or larger sized ungulate species (Cohen *et al.* 1978; Grassman *et al.* 2005b; Kamler *et al.* 2012; Selvan *et al.* 2013a; Selvan *et al.* 2013b; Selvan *et al.* 2013c; Hayward *et al.* 2014; Aryal *et al.* 2015).

Clouded leopard

The mainland clouded leopard *Neofelis nebulosa*, a species with a range restricted to mainland Southeast Asia, and is classified as Vulnerable by the IUCN (Grassman *et al.* 2016a). The

clouded leopard weighs between 11 to 20 kg (Grassman *et al.* 2005a); it has stout legs with broad paws which are good for climbing trees and getting around thick forest; and it is known to be highly arboreal (Sunquist and Sunquist 2002). The clouded leopard is strongly associated with primary evergreen tropical forest at elevations up to 3000 m, but their presence has also been recorded in dry, deciduous, secondary and logged forest (Rabinowitz *et al.* 1987; Grassman *et al.* 2005a; Austin *et al.* 2007). Unlike dhole, clouded leopard is solitary hunter and preys upon a variety of arboreal and terrestrial prey species such as birds, primates, ungulates and rodents (Nowell and Jackson 1996; Grassman *et al.* 2005a). The species was also recorded predating on a binturong *Arctictis binturong* (Lam *et al.* 2014). A study by Ngoprasert *et al.* (2012) in Thailand found that occurrence of clouded leopard was associated with habitat where red muntjac and wild pig were most likely to be present.

Asian golden cat

The Asian golden cat *Catopuma temminckii* is a medium sized felid (9-16 kg) with a wide distribution range across Southeast Asia (Sunquist and Sunquist 2002), and is classified as Near Threatened by the IUCN (McCarthy *et al.* 2015a). Based on genetic analysis, this species was thought to be closely related to the marbled cat (Johnson *et al.* 2006c), but the recent assessment of skull morphology suggested the two species should be put in separate families (Sicuro and Oliveira 2011). The Asian golden cat is primarily found in tropical and subtropical moist evergreen, mixed evergreen, and dry deciduous forests. (Nowell and Jackson 1996; McCarthy *et al.* 2015b). Based on the radio collaring results of a male and a female, they were found most often in closed forest habitats (Grassman *et al.* 2005a). The species was also recorded in other habitat types such as shrub, grasslands, and degraded forest (Duckworth *et al.* 1999b; Duckworth *et al.* 2005; Grassman *et al.* 2005a; Wang 2007a). The Asian golden cat has been recorded in a wide range of elevation; from lowland forest up to about 3,900m (McCarthy *et al.* 2015a).

Marbled cat and leopard cat

The marbled cat *Pardofelis marmorata* (2-5 kg) and the leopard cat *Prionnailurus bengalensis* (3-7 kg) (Sunquist and Sunquist 2002) partly overlap in range although the latter is more widely spread across Asia (Ross *et al.* 2015; Ross *et al.* 2016). Reports by Grassman *et al.* (2005a) and Rajaratnam *et al.* (2007) from Thailand and Borneo (Malaysia) suggest similar habitat type use (deciduous forests, tropical evergreen forests, scrub, bamboo regrowth, degraded forests, and grassland) by both species, but with the marbled cat showing a strong preference for forest habitats and the leopard cat for open habitats including plantations. Despite some arboreal tendencies, the marbled cat spends most of its time on the ground (Grassman *et al.* 2016b). They can be found in habitats with elevation up to 3000m (Ross *et al.* 2015). The IUCN classifies the marbled cat as Vulnerable (Ross *et al.* 2016) and the leopard cat as Least Concern (Ross *et al.* 2015) with habitat loss to deforestation, prey depletion and illegal hunting being main threats for both species. Leopard cat is facing local extinction in parts of its range (Ross *et al.* 2015; Ross *et al.* 2016).

Research Questions

To address the overarching aim, this project seeks to investigate the following specific research questions.

What is the diversity of carnivores and prey species in NEPL after a decade of protected area management? In particular, have globally important populations of the three apex carnivores, E tiger, CE Indochinese leopard and E dhole, been conserved?

Snaring has been increasing in the NEPL (Johnson *et al.* 2016) and throughout SE Asia (Gray *et al.* 2017a) which is causing dramatic declines in populations of the tiger and leopard in the region. The NEPL has been actively managed since 2003 but it also undergone various changes in its management structure over the past decade (Johnson 2012). The NEPL contained the last

remaining population of the tiger in Laos, and a major goal of management was to conserve this globally important tiger population. The impacts of management on species diversity in NEPL, including tiger, other endangered carnivore and prey species, had not been assessed since 2003-2004. An updated assessment of species diversity would not only determine the current status of tiger and other endangered species in NEPL, but it would also measure the effectiveness of a decade of active management that specifically focused on the conservation of the tiger and its prey.

What are the density trends of small and meso-felids in NEPL? Is there any evidence of interactions between them?

The mesopredator release hypothesis (Soulé *et al.* 1988) predicts that when top predators are removed from a system the mesopredators increase in number and consequently have a negative effect on the small predators and prey (Berger *et al.* 2008). The effect is manifested by a carnivore community with few top predators, elevated abundances of mesocarnivores, and low numbers of small carnivores. However, given the rise in indiscriminate snaring in NEPL, any effects of mesopredator release might be overridden by such human-induced disturbance to species numbers.

What is the spatial and temporal activity pattern and overlap of the five sympatric carnivores in the NEPL NPA?

According to Hardin (1960), to promote coexistence and limit the negative effects of competition on fitness, competitors are necessarily required to have some level of ecological differences because competitors cannot coexist completely (Gause 1934; Macarthur and Levins 1967). When resources are limited, competition between species becomes prominent. However, the intensity of interspecific competition should depend largely on the degree of niche overlap or the similarity of habitat requirements between the two species. It is suggested that when

species are ecologically similar, they partition their temporal activity to avoid encounters during foraging and thereby facilitate their coexistence (e.g., Di Bitetti *et al.* 2009; Lucherini *et al.* 2009). Determining the spatial and temporal overlap of key carnivore species is important for understanding their ecological roles in ecosystems, and their relationships with each other, which ultimately can aid in their conservation.

Where are the most suitable areas for conservation of felids and dhole concentrated in Lao PDR?

Detailed knowledge about the geographic occurrence of key species is required as part of a suite of tools to support the development of effective conservation measures (Kaschner *et al.* 2006). When resources for species conservation are limited, careful and effective conservation planning is required which often involves prioritization of management areas and identification of the best possible means to use limited resources in an efficient manner (Pressey and Bottrill 2009). Creating national maps showing the suitability of key carnivore species will assist conservation efforts at the national and local levels and can help lead to the development of species' national management plans. By focusing of the largest carnivores remaining in the country, conservation and management plans for these species can act as an umbrella for conserving many other species.

Approaches used to address the aforementioned research questions are detailed in the following chapters.

Thesis Overview

Chapter 2: Documenting the Demise of Tiger and Leopard, and the Status of Other Carnivores and Prey, in Lao PDR's Most Prized Protected Area: Nam Et - Phou Louey

This chapter assessed the most recent status of the carnivores and prey species based on three surveys undertaken between 2013 and 2017, to further assess the outcome of conservation management and provide a new baseline for future wildlife management planning and action in the NEPL. Here, species relative degree of commonness was inferred through hierarchical multispecies occupancy models developed by Dorazio and Royle (2005) and Dorazio *et al.* (2006; 2010), which allowing occupancy at the levels of both individual species and communities to be modelled, while accounting for specific detection probabilities (Kéry and Royle 2016).

Chapter 3: Density trends of Small and Meso-Felids in Nam Et - Phou Louey National Protected Area, Lao PDR

The focus of this chapter was on density estimation of small and meso-felids with unique pelage (i.e., marbled cat, leopard cat and clouded leopard) in NEPL NPA. Density trend over study period from 2013 to 2017 was assessed in order to examine interactions amongst themselves as well as assessing whether mesopredator release occurred after the disappearance of tiger.

Chapter 4: Spatial co-occurrence and activity patterns of sympatric felids and dholes in Nam Et - Phou Louey National Protected Area, Lao PDR.

In order to investigate spatial and temporal dimension of niche segregation in detail, this chapter examined factors influencing species occupancy, tested for influence of dominant species on subordinate species. Activity patterns and overlap amongst the sympatric carnivores also was investigated, and dietary overlap was inferred from the literature. Findings then allowed for inference of coexistence mechanisms used by the sympatric carnivores.

Chapter 5: **Conservation priority landscape for meso-felids and dholes in Lao PDR**

This chapter focused on mapping the distribution of meso-felids (clouded leopard and Asian golden cat) and dhole with the aim to provide a tool to guide conservation planning of carnivore conservation across Laos. Results from Chapter 4 was used to predict suitable habitat of the three species for the whole country to highlight potentially important conservation areas, which ultimately will assist not only carnivore conservation but also the conservation of many other species in the country.

Chapter 6: **General discussion**

This chapter summarised, synthesised and discussed findings from chapters 2 – 5. Discussion of results, implication and recommendations for future improvements for data collection and analysis were included in this section.

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Chapter 2

Documenting the Demise of Tiger and Leopard, and the Status of Other Carnivores and Prey, in Lao PDR's Most Prized Protected Area: Nam Et - Phou Louey

Submitted to *Global Ecology and Conservation*

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Abstract

The Nam Et - Phou Louey National Protected Area (NEPL) is known for its diverse community of carnivores, and a decade ago was identified as an important source site for tiger conservation in Southeast Asia. However, there are reasons for concern that the status of this high priority diverse community has deteriorated, making the need for updated information urgent. This study assesses the current diversity of mammals and birds in NEPL, based on camera trap surveys from 2013 to 2017, facilitating an assessment of protected area management to date. We implemented a dynamic multispecies occupancy model fit in a Bayesian framework to reveal community and species occupancy and diversity. We detected 43 different mammal and bird species but failed to detect leopard *Panthera pardus* and only detected two individual tigers *Panthera tigris*, both in 2013, suggesting that both large felids are now extirpated from NEPL, and presumably also more widely throughout Laos. Mainland clouded leopard *Neofelis nebulosa* had the highest estimates of probability of initial occupancy, persistence and colonization, appearing to be the most widely distributed large carnivore, followed by dhole *Cuon alpinus*. Both of these species emerge as a priority for further monitoring and conservation in the NEPL landscape. This study provides the most recent assessment of animal diversity and status in the NEPL. Our analytical approach provides a robust and flexible framework to include sparse and inconsistent data sets of multiple species to assess their status via occupancy as a state process, which can often provide insights into population dynamics.

Key-words: clouded leopard; dhole; dynamic multispecies occupancy model; Laos; Nam Et - Phou Louey National Protected Area; tiger.

1. Introduction

The Nam Et - Phou Louey National Protected Area (hereafter NEPL) in northern Lao PDR (hereafter Laos) is known for its high biodiversity including a rich carnivore community (Johnson *et al.* 2006). A decade ago NEPL was considered home to one of the most important tiger populations in all of Laos, Cambodia, and Vietnam, and an important source site for tiger conservation in Southeast Asia (Walston *et al.* 2010). However, the current situation is unknown, and there is widespread concern that poaching may be reaching unsustainable levels (Gray *et al.* 2017b). Surveys in the 1990s suggested that NEPL has been found to hold most of the species of bird and large mammal that would be expected on biogeographic and habitat grounds, comprising 6 felid species, dhole, *Cuon alpinus*, 2 bear species, Asian elephant, *Elephas maximus*, 14 other small carnivore species, 7 ungulate species, 5 primate species, and 299 bird species (Johnson 2012). The first systematic camera trap surveys were conducted during 2003 to 2004 to determine the baseline of large carnivore and prey species (Johnson *et al.* 2006b) together with subsequent surveys up until 2008 confirmed the presence of the aforementioned carnivore, ungulate, primate and some smaller mammal species. Unregulated over-harvesting of animals and plants as well as loss of forest to agricultural expansion are the main threats to wildlife of the NEPL (Johnson 2012). Factors suspected to undermine efforts to protect NEPL's wildlife include turnover of staff in the protected area and funding uncertainties. The study by Johnson *et al.* (2016) suggested a decline in abundance of tiger (*Panthera tigris*) and an increase in the abundance of some large ungulate prey over a period of seven years (2005 to 2012) during the implementation of a new law enforcement strategy. In this study, we add more recent data from the largest camera trapping effort ever conducted in Laos and assess the most recent status of the carnivores and prey species based on three surveys undertaken between 2013 and 2017. We thereby assess the outcome of protected area management and provide a new baseline for future wildlife management planning and action in the NEPL.

Of all the biodiversity in NEPL, this site has earlier been recognized as globally important for conserving breeding populations of the Endangered tiger (Johnson 2012), and Endangered dhole (Kamler *et al.* 2012). In fact, NEPL was thought to harbour the last breeding population of tigers in Indochina (Johnson *et al.* 2016), and was identified as one of the most important source sites for tiger conservation in Southeast Asia (Walston *et al.* 2010). Additionally, based on 2000s surveys, it was hoped that NEPL would retain a leopard population, of which only one other is known in all of Cambodia, Lao and Vietnam. Management and enforcement policies in NEPL during the past 10 years have focused on conserving the tiger, but it is unclear whether these interventions have succeeded in conserving these globally important populations of tigers, leopards, and dholes.

According to Peet (1974), diversity has two components: (i) species richness (the number of species that live in a specific area); and (ii) species evenness (or relative degrees of commonness and rarity of the species in the community). Although species richness is very widely used as a measure of biological diversity, it alone does not indicate the health of an ecosystem because diversity indices can remain high despite the extinction of some rare species (Travaini *et al.* 1997). Therefore, auditing the status of an area's diversity necessitates knowledge of both species abundance (e.g., occupancy as a proxy) and richness. We infer the relative degree of species commonness through hierarchical multispecies occupancy models, which allow us to estimate and model occupancy at both individual and communities levels, while accounting for species-specific detection probabilities (Kéry and Royle 2016). It also enables us to evaluate changes in species composition and occupancy in multiple areas over time (Tobler *et al.* 2015).

2. Materials and Methods

2.1. Study Area

The NEPL is the largest protected area in Laos, covering 5,969 km^2 of mountainous terrain across seven districts and three provinces (Houaphan, Luang Prabang, and Xiengkhuang). It is located in the northern highlands of Laos (between latitude 19°50' - 20°50'N and longitude 103°00' - 103°53'E), bordering Vietnam along its northern boundary (Fig. 1). NEPL has an elevation ranging from 400 - 2257 m and is largely dominated by dry evergreen and semi-evergreen forests (Johnson 2012). However, around one third of the park is degraded forest with a canopy cover of less than 20%. The area has a tropical monsoonal climate with a rainy season lasting from May to October (with annual rainfall of 1400 to 1800 mm), followed by a distinct dry season for the remainder of the year (Johnson 2012).

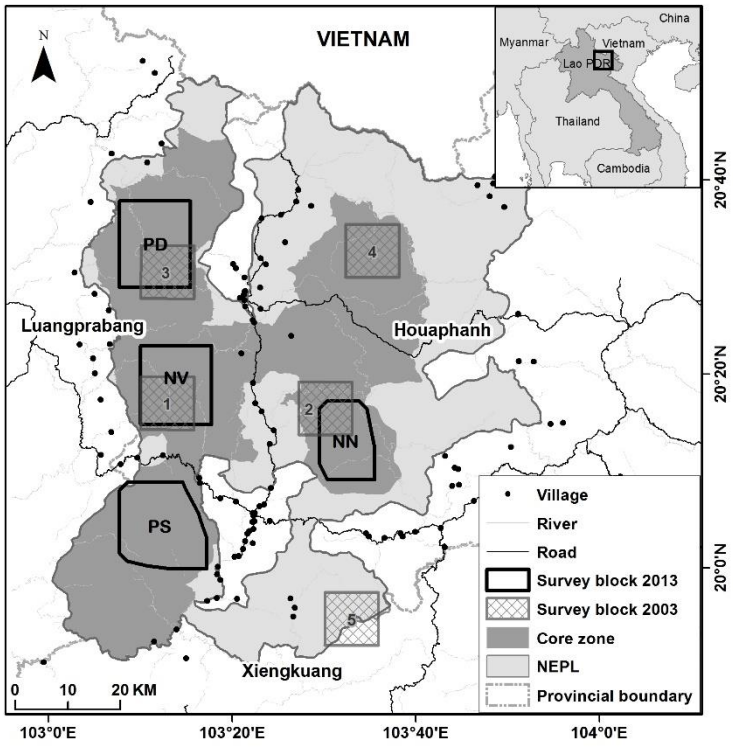


Fig. 1. The Nam Et - Phou Louey National Protected Area (NEPL), Laos, with 2013 - 2017 survey blocks (NV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; and NN = Nam Neun) and the 2003 - 2006 survey blocks (numbered from 1 – 5).

The NEPL is divided into a totally protected core zone where human activity is prohibited, and a managed use zone (Fig.1). There are approximately 94 villages situated in, or within 10 km of, the core zone boundary (Johnson 2012). Their livelihood activities, which include illegal hunting for trade using modern equipment (e.g., wire snares and guns), and gathering of other non-timber forest products, shifting cultivation and livestock raising, undoubtedly pose stresses to the NEPL wildlife population.

2.2. Data Collection

Systematic camera trap surveys were carried out within the NEPL core zone from 2013 to 2017 in four blocks of ~200 km^2. The Nam Poung - Na Vaen (NV) area (Fig.1) is mainly dominated by semi-evergreen and evergreen forest. This block almost completely covered the sampling Block 1 of the previous surveys between 2003 and 2004 (Johnson *et al.* 2006b). The Pha Daeng (PD) area is mainly dominated by semi-evergreen forest and grassland and covered 80% of the sampling Block 3 of the previous survey (Fig. 1). The Phoupha - Siphou (PS) area is dominated by semi-evergreen forest with a small mixture of evergreen forest and patches of grassland. The Nam Neun (NN) area is defined by low density semi-evergreen forest with patches of high density semi-evergreen forest and shrub/bamboo forest. This is the smallest block, measuring 145 km^2 and overlapping Sampling Block 2 of the previous survey by about 50% (Fig. 1).

For NV, PD and PS blocks, camera traps were set in pairs at 80 locations at 1–1.5 km spacing between locations. The surveys were repeated three times (Table 1). We used a mixture of infrared camera trap models: CuddeBack Ambush IR – Model 1187, Reconyx Hyperfire HC500, and MAGINON–WK 3 HD camera traps. The NN block contained 60 camera trap sites and was surveyed in only one year (Table 1).

Traps were located at between 629 – 2,185 m altitude: 16% were below 1,000 m, 16% between 1,000 to 1,500 m, and 68% above 1,500 m. About 63% of the sites were in closed forest –

evergreen and high density semi-evergreen forests. The camera traps were placed mostly along ridgelines and animal trails, and at points where trails meet streams. Each camera was set without baits at 35 cm above the ground and was set to work throughout the 24-hr cycle. Each survey period lasted for a minimum of 49 days.

Table 1: Camera trap survey dates, effort and altitude in four blocks in Nam Et - Phou Louey, Laos, during 2013 - 2017

Block, site name	Survey name	Date	Duration (days)	Station (cameras)	Trap days	Altitude (m)
1, Nam Poung - Na Vaen						
	NPNV1	3-5/2013	53	80 (160)	3831	983 - 2185
	NPNV2	3-5/2015	52	80 (158)	3200	
	NPNV3	2-4/2017	52	80 (156)	3530	
2, Pha Daeng						
	PD1	11/2013 – 1/2014	51	80 (159)	3693	709 - 1739
	PD2	5-7/2015	51	80 (156)	3282	
	PD3	4-5/2017	50	80 (160)	3240	
3, Phoupha - Siphou						
	PS1	2-4/2014	54	80 (160)	3446	629 - 1514
	PS2	2-4/2016	50	80 (160)	3003	
	PS3	6-8/2017	49	80 (160)	1977	
4, Nam Neun	NN1	5-7/2014	54	60 (120)	2825	720 - 1522

2.3. Data Organisation and Preparation

Each camera-trap photo of an animal was identified, and organised using the CamtrapR (Niedballa *et al.* 2016). Notionally independent events, following O'Brien *et al.* (2003), were used for our analysis. We included records from a total of 43 species including: large to small-sized carnivores, ungulates, primates, birds and other small mammals (Table 2). The species were also grouped based on their primary diet guilds which are carnivore, herbivore, insectivore and omnivore. To reduce heterogeneity and reduce the computational burden of model fitting, we aggregated our data into 10-day sampling occasions; there were a total of five occasions per year.

2.4. Data Analysis

We implemented a dynamic community model (DCM) as described in Kéry and Royle (in prep), also known as a dynamic multispecies occupancy model (Dorazio *et al.* 2010) in a Bayesian framework. In common with other occupancy models, the main assumptions of a DCM within each primary period are: (i) no extinction and colonisation at the stations over replicated secondary periods (but both are allowed between primary periods); (ii) all detected species are correctly identified; and (iii) the detection probability and occupancy at a station are independent of detection and occupancy at another station (Iknayan *et al.* 2014).

Although our data set is the result of an immense field effort and comprises thousands of photographs, statistically it is still sparse. Hence, we did not employ data augmentation (Kéry and Royle 2016) in the analysis of our DCM , since it could lead to unrealistically high estimates of species richness (Guillera-Arroita *et al.* 2019). Hence, species richness estimates will refer to a maximum of 43, which is the list of species observed in our study. The DCM can formally be described in simple stages:

Initial state for species *k*: $z_{i,1,k} \sim Bernoulli(\Psi_k)$

State dynamics for species *k*: $z_{i,t+1,k}|z_{i,t,k} \sim Bernoulli(z_{i,t,k}\phi_k + (1 - z_{i,t,k})\Upsilon_k)$

Observation process for species *k*: $y_{i,t,k}|z_{i,t,k} \sim Binomial(z_{t,k}p_{i,k})$

In this model $z_{i,t,k}$ is the true presence/absence state of species *k* at camera station *i* during primary period *t* and $y_{i,\,t,\,k}$ are the observed data: the detection frequencies, or the sum of sampling occasions out of five annual occasions that the species *k* was detected at station *i* in year *t*. The model has four primary parameters psi (ψ), phi (ϕ), gamma (Υ), and *p* denote the probability of initial occupancy, persistence, local colonisation and detection, respectively. Initial occupancy is the probability that species *k* is occurring at station *i* during time period one. Persistence is the probability of station *i* remaining occupied by species *k* during period *t+1* given that the species was present during the previous period. Colonization is the probability that the station *i* becomes occupied by species *k* during period *t+1* given that the species was absent during the previous period. Probability of detection is the probability of detecting species *k* at station *i* given that the species is actually present.

We accounted for heterogeneity between 43 recorded species by fitting separate parameters for each species and treating these parameters as random effects, with hyperparameters that are estimated from the data and which formally describe the entire community of the 43 species detected during our study. Thus, in our model we created a link between the parameters of each species and the parameters that describe the community by assuming that the species-level parameters (on the logit scale) were draws from a Normal distribution,

$$\theta_k \sim Normal(\mu_\theta, \sigma^2_\theta)$$

where θ stands for any of the four primary parameters in the model. The parameters of the Normal distribution describe the community from which the 43 study species are assumed to be sampled from, such that μ_θ is the community average for θ (it could also be thought of as

the value for the average species) and σ_θ^2 is the variance among species in that parameter. Thus, the mean hyperparameter describes the central tendency of the parameter values among all species in the community, while the variance hyperparameter describes the heterogeneity among species in that parameter.

In addition, we had to account for possible non-independence of parameters owing to the clustering of camera trap stations in the four blocks *b*, in which the 300 stations were nested. Due to the fact that the 300 data points are not independent, but instead there is a dependency due to the blocking in our study, we therefore accounted for this by adding random block effects in only initial occupancy and detection. For computational parsimony, for each species, we fitted a single block effect for detection for all years instead of fitting a separate block effect in every year (and for every species). Also for parsimony, we did not fit block effects in persistence and colonization parameters. We also assumed that guild *g* (four diet guilds) affected the mean of the parameters for species, but that it does not affect the heterogeneity among species. To account for this assumption, instead of fitting a single Normal distribution for each parameter type (to present species-by-species variability in ψ, φ, Υ or *p*), as shown above, we estimated four such Normal distributions for each parameter where the mean of the four is different, but the variance is identical. Therefore, submodels for initial occupancy probability, persistence, colonisation and detection can be described as follows (where the modelling is applied on the logit scale, as customary for data such as ours):

The submodel for initial occupancy had the sum of $lpsi1_k$ and $lpsi.block_{block_i,k}$ on the logit scale, i.e., a species-specific intercept and species-specific random block effect. Both are assumed to be drawn from two Normal distributions with a mean and standard deviation hyperparameters.

$$logit(\psi_{i,k}) = lpsi1_k + lpsi.block_{block_i,k}$$

$$lpsi1_k \sim Normal(mu.lpsi1_{guild_k},\ sig.lpsi1)$$

$$lpsi1.block_{b,k} \sim Normal(0,\ sig.lpsi1.block_k)$$

The submodels for persistence and colonization were similar, but lacked a block effect (for computational reasons in our relatively sparse data set).

For persistence:

$$logit(\phi_{i,k}) = lphi_k$$

$$lphi_k \sim Normal(mu.lphi_{guild_k},\ sig.lphi)$$

For colonisation:

$$logit(\gamma_{i,k}) = lgamma_k$$

$$lgamma_k \sim Normal(mu.lgamma_{guild_k},\ sig.lgamma)$$

Finally, the submodel for detection was analogous to that for initial occupancy:

$$logit(p_{i,k}) = lp_k + lp.block_{block_i,k}$$

$$lp_k \sim Normal(mu.lp_{guild_k},\ sig.lp)$$

$$lp.block_{b,k} \sim Normal(0,\ sig.lp.block_k)$$

Estimates of species richness were derived from the posterior distribution of *z*, i.e., the presence/absence indicators for every species, site and year. The posterior distributions of our model parameters were estimated using Markov Chain Monte Carlo implemented in JAGS

(version 4.2.0) through program R (jagsUI; Kellner 2015). The model was run for 3 parallel chains with 100,000 values retained per chain after discarding 50,000 for adaptation and burn-in, and thinning by 10. We assessed convergence using the Gelman-Rubin statistic where value <1.1 denotes convergence (Gelman and Rubin 1992). We calculated the Bayesian P-value of the model to assess its goodness-of-fit based on the Freeman-Tukey statistic (Freeman and Tukey 1950). Based on Gelman-Rubin diagnostics, there was no evidence of the lack of convergence for our model.

3. Results

3.1. Raw data summaries

Over the 32,027 trap nights of our total survey effort, in total 9,762 notionally independent encounters of wildlife were recorded (Table 1). From these records, 43 different species were detected (Table 2). These include 5 species of cats, dhole, 2 species of bear, 11 species of small carnivores (mustelids, civets, mongooses and spotted linsang), 6 ungulate species, 4 species of macaques, and 14 other prey species (small mammals and birds). Importantly, Tiger was detected only in the first year of the surveys (in 2013), but not in later years of our study (Table A.1). The leopard *P. pardus* was not detected during our study.

Table 2: Mammals and birds recorded during camera trap surveys from 2013 to 2017 in Nam Et - Phou Louey National Protected Area, Laos.

				Sampling block			
Family	**Scientific name**	**Common name**	**Status***	**NV**	**PD**	**PS**	**NN**
Bovidae	*Bos gaurus*	Gaur	VU	x		x	
	Capricornis milneedwardsii	Indochinese serow	NT	x	x	x	x
Canidae	*Cuon alpinus*	Dhole	EN	x	x	x	x
Cercopithecidae	*Macaca assamensis*	Assamese macaque	NT	x	x	x	x
	Macaca leonina	Northern pig-tailed macaque	VU	x	x	x	
	Macaca mulatta	Rhesus macaque	LC	x	x	x	x
	Macaca arctoides	Stump-tailed macaque	VU	x	x	x	x
Cervidae	*Muntiacus vaginalis*	Northern red muntjac	LC	x	x	x	x
	Cervus unicolor	Sambar	VU	x	x	x	x
	M. rooseveltorum complex	Small dark muntjac(s)	DD	x	x	x	x
Felidae	*Catopuma temminckii*	Asian golden cat	NT	x	x	x	x
	Neofelis nebulosa	Mainland clouded leopard	VU	x	x	x	x
	Prionailurus bengalensis	Leopard cat	LC	x	x	x	x
	Pardofelis marmorata	Marbled cat	VU	x	x	x	x
	Panthera tigris	Tiger	EN	x	x		
Herpestidae	*Herpestes urva*	Crab-eating mongoose	LC	x	x	x	x
Hystricidae	*Atherurus macrourus*	Asian brush-tailed porcupine	LC	x	x	x	x
	Hystrix brachyura	East Asian porcupine	LC	x	x	x	x

Muridae	*Leopoldamys sabanaus*	Long-tailed giant rat	LC	x	x	x	
	Rattus exulans	Pacific rat	LC	x	x	x	
	Rattus nitidus	White-footed Indochinese rat	LC	x	x		
Mustelidae	*Melogale* complex	Ferret badger(s)	LC	x	x	x	
	Arctonyx collaris	Greater hog badger	VU	x	x	x	x
	Martes flavigula	Yellow-throated marten	LC	x	x	x	x
Phasianidae	*Polyplectron bicalcaratum*	Grey peacock pheasant	LC	x	x	x	x
Prionodontidae	*Prionodon pardicolor*	Spotted linsang	LC	x	x	x	
	Lophura nycthemera	Silver pheasant	LC	x	x	x	x
	Gallus gallus	Red junglefowl	LC	x	x	x	x
	Arborophila rufogularis	Rufous-throated partridge	LC	x	x	x	
Sciuridae	*Petaurista philippensis*	Indian giant flying squirrel	LC	x			
	Ratufa bicolor	Black giant squirrel	NT	x	x	x	
	Tamiops complex	Striped squirrel(s)	LC			x	
	Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	LC	x	x	x	
	Dremomys rufigenis	Red-cheeked squirrel	LC	x	x	x	
Suidae	*Sus scrofa*	Eurasian wild pig	LC	x	x	x	x
Ursidae	*Ursus thibetanus*	Asian black bear	VU	x	x		x
	Helarctos malayanus	Sun bear	VU	x	x	x	x
Viverridae	*Arctictis binturong*	Binturong	VU	x	x	x	
	Paradoxurus hermaphroditus	Common palm civet	LC	x	x	x	x
	Viverra zibetha	Large Indian civet	LC	x	x	x	x

Paguma larvata	Masked palm civet	LC	x	x	x	x
Chrotogale owstoni	Owston's civet	EN	x	x		
Viverricula indica	Small Indian civet	LC	x	x	x	

NV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; NN = Nam Neun

*Based on IUCN Red List of Threatened Species, LC = Least concern; NT = Near threatened; VU = Vulnerable; EN = Endangered.

3.2. Species and community inferences using the dynamic community model

The dynamic community model for multispecies provided estimates of predicted detection probability, initial occupancy, rate of persistence and colonization, corrected for imperfect detection, for each of the 43 species. Additionally, the mean estimates of each of these parameters for each of the four diet guilds (i.e., carnivore, herbivore, insectivore and omnivore) were also produced as a result of the model.

3.2.1. Species and Dietary Guild Group Initial Occupancy, Persistence and Colonization

The estimated mean of initial occupancy for tiger was 0.20 ± 0.21 Standard Deviation (95% Bayesian credible interval 0.001, 0.71), however, its probability of persistence and colonization estimates were lowest in the carnivore category (Fig.2.a, b, c). Mainland clouded leopard *Neofelis nebulosa* had the highest estimates in probability of initial occupancy, persistence and colonization (0.51 ± 0.18 [0.18, 0.88]; 0.54 ± 0.13 [0.29, 0.79]; 0.51 ± 0.17 [0.23, 0.87], respectively), compared with the rest of the carnivore category (Fig.2.a, b, c). Dhole had the second highest in initial occupancy 0.39 ± 0.15 (0.13, 0.69) but its rate of persistence was as low as that of the tiger (Table A.2 and Table A.3). Interestingly, dhole had rate of colonization about 20 times higher than tiger (see Table A.4). Estimated initial occupancy of Asian golden cat 0.38 ± 0.13 (0.12, 0.63) was similar to that of the dhole. Although the rate of persistence of the Asian golden cat was slightly higher, its colonization rate was half that of dhole. Surprisingly, the initial occupancy estimates for leopard cat and marbled cat were almost as low as that of the tiger 0.20 ± 0.09 (0.04, 0.37) and 0.23 ± 0.13 (0.02, 0.48), except that their rates of persistence were twice as high and rates of colonization were 15 times higher than that of the tiger (see Table A.3 and Table A.4).

Among the small, non-felid carnivores, yellow-throated martens had the highest mean initial occupancy and persistence estimates, followed closely by greater hog badger, but their rates of colonization were less than those of masked palm civet (Fig.2.a & b). The common palm civet

was shown to have the lowest estimates for initial occupancy and persistence, but its colonization rate however was 30-fold higher than the initial occupancy. Overall, apart from yellow-throated marten and greater hog badger, the estimated means of initial occupancy for other species in this group were still lower than 0.5. None of the small, non-felid carnivores had mean estimates of greater or equal to 0.5 for persistence and colonization (Fig.2.b & c).

Of the two bear species detected during the survey, the estimated mean of initial occupancy, persistence and colonization for sun bear *Helarctos malayanus* were higher than the estimates for Asian black bear *Ursus thibetanus* (Fig.2.a, b, c). However, their estimated means of initial occupancy were fairly low and even lower than the mean estimate for the tiger and other cats. Interestingly, the estimated rate of persistence and colonization for both bear species were much higher, compared to the mean estimates for tiger (Fig.2.b, c).

Among the prey species, northern red muntjac *Muntiacus vaginalis* had the highest mean of initial occupancy, persistence and colonization, as the estimates for all three parameters for this species are above 0.6. Stump-tailed macaque *Macaca arctoides* had the second highest estimates, especially for initial occupancy and colonisation rates. Eurasian wild pig *Sus scrofa* had the third highest mean estimate of initial occupancy but its rates of persistence and colonisation were about 2 – 3 times lower than those of red muntjac. For the small dark muntjac *M. rooseveltorum* complex, its initial occupancy was about 5 times lower than that of the red muntjac, its rate of persistence however is slightly above 0.5 and its colonization rate was slightly higher than that of Eurasian wild pig. Among small mammal prey species, East Asian porcupine *Hystrix brachyuran* had the highest mean estimates of initial occupancy, persistence and colonization. In the insectivore or bird group of prey species, silver pheasant had the highest mean estimates of initial occupancy and colonization with the persistence rate of slightly above 0.5 (Fig.2.a, b, c). The model results showed very low estimates of all three parameters for large ungulate species (i.e., gaur, sambar and Indochinese serow) and other small mammals such as squirrels and rats (Fig.2.a, b, c and Table A.2, 3, 4).

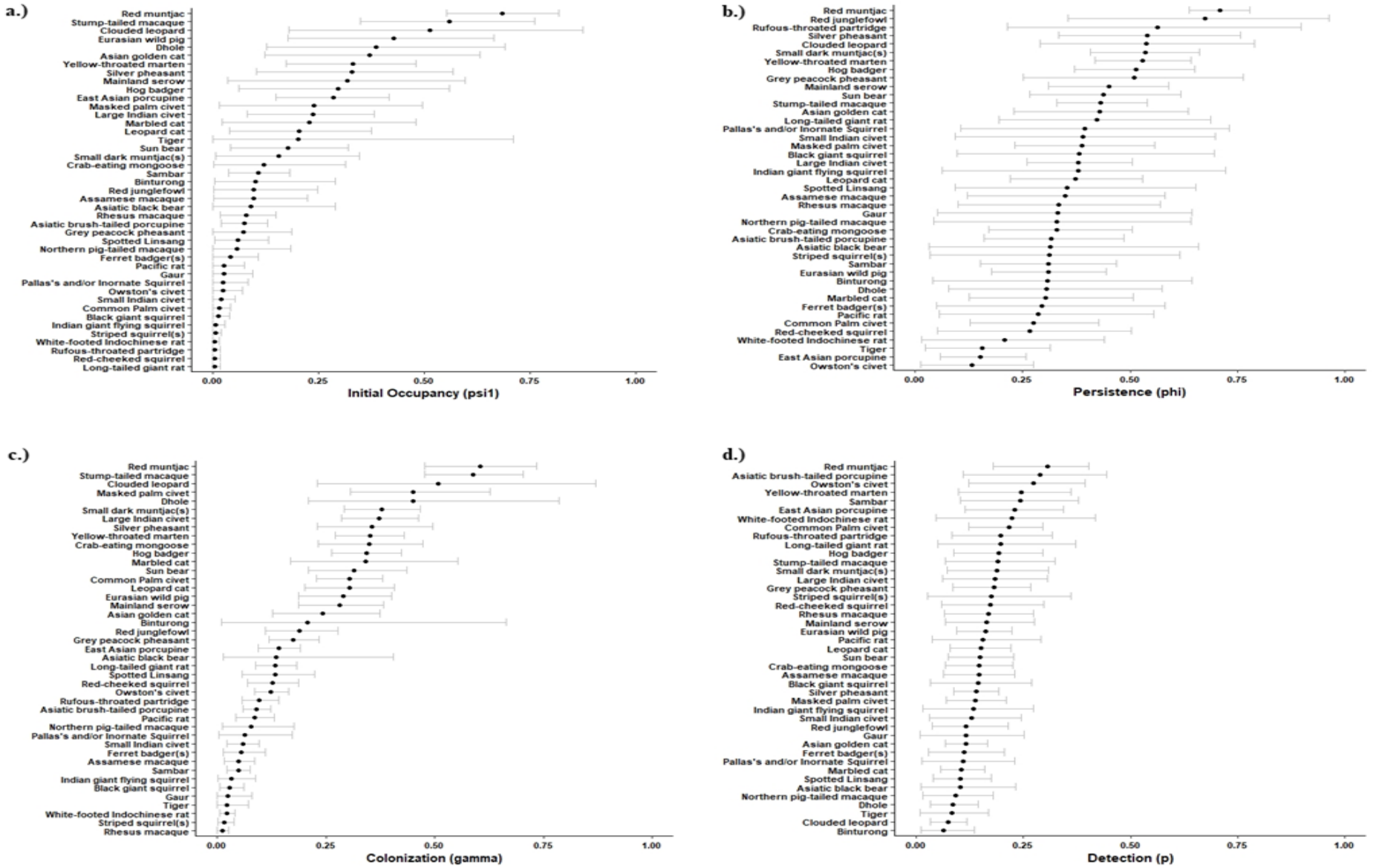


Fig. 2. Plots of estimated mean detectability, occupancy, persistence and colonization of species detected in Nam Et - Phou Louey, Laos, during 2013 - 2017

At the dietary guild level, carnivores and insectivores had the same initial occupancy rates and were higher than omnivores and herbivores. However, the initial occupancy values of all groups were well below 0.5 (Fig.3.a). In terms of the probability to persist, insectivores were highest among the groups followed by carnivores, and then herbivores and omnivores. There was a very minimal difference among the estimated mean probability of colonization for carnivores, insectivores and omnivores whereas herbivores had the lowest estimated probability. Despite some differences in the probability of colonization, the mean estimates for all groups were considerably low and below 0.3.

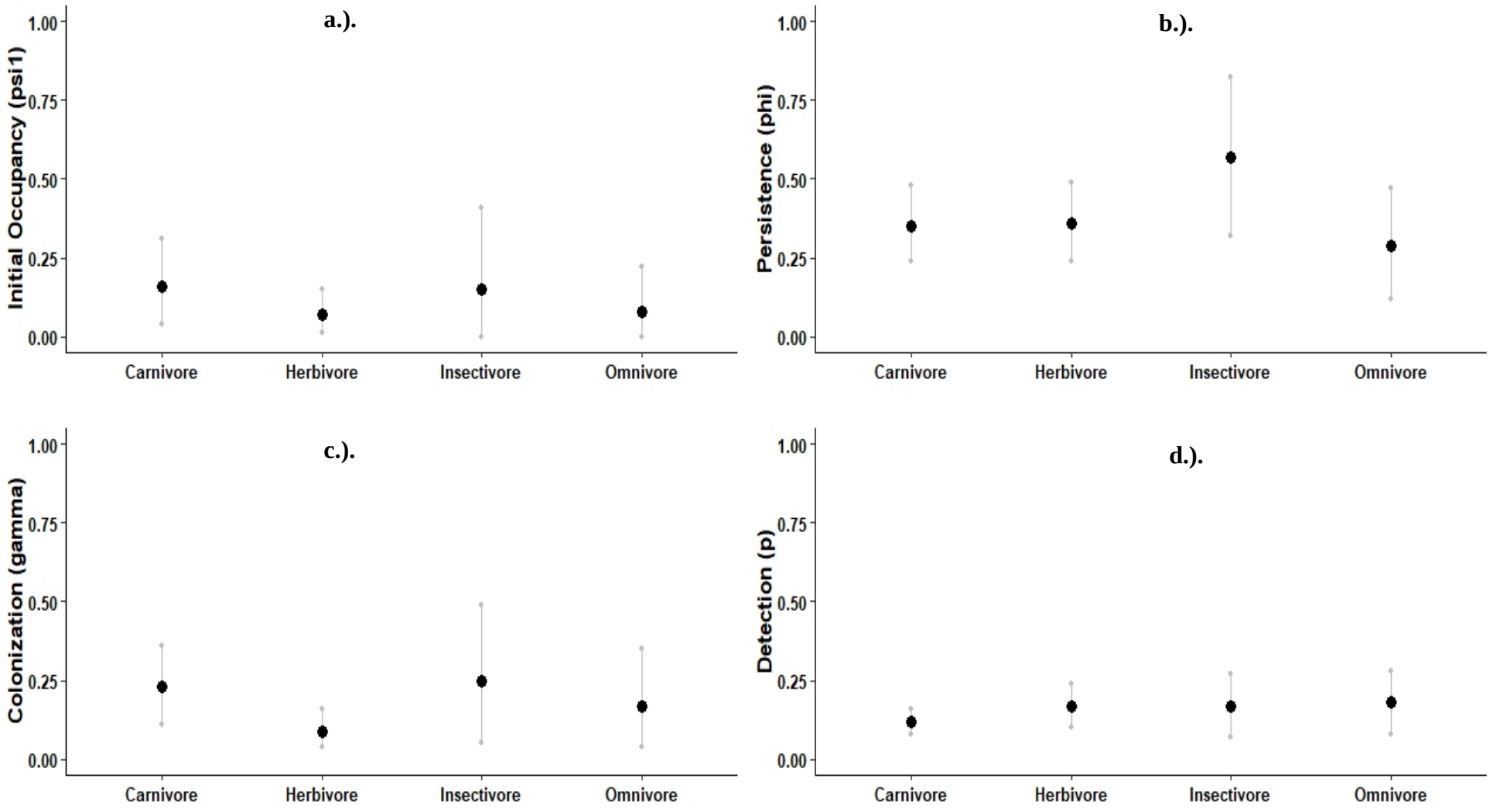


Fig. 3. Plots of estimated mean detectability, occupancy, persistence and colonization of four dietary guilds in Nam Et-Phou Louey, Laos, during 2013 – 2017.

3.2.2. Species and Dietary Guild Group Detectability

The estimated means of detection probability varied slightly among the species and overall estimates were below 0.5 (Fig. 2.d). At the diet guild level, carnivores had the lowest estimated detection probability 0.12 ± 0.02 (0.08, 0.16). While the estimates of detection probabilities for the other three guild groups were slightly higher, the differences among all dietary guilds were seemingly minimal to non-existent (Fig.3.d). Amongst carnivores detected, the yellow-throated marten *Martes flavigula* had the highest detection probability with binturong *Arctictis binturong* having the lowest rate of detection (see Table A.5). There were no differences in the mean detection probability amongst any of the felids or dhole. The main pattern is that small carnivores had higher detection probabilities than large and medium sized-carnivores (Fig. 2.d). Amongst the large and medium-sized prey species, red muntjac, Asian brush-tailed porcupine *Atherurus macrourus*, sambar *Cervus unicolor* and East Asian porcupine *Hystrix brachyura* had the highest estimated detection probability (see Table A.5).

3.3. Species Richness

The number of species estimated to occur each year varied little. Of 43 species examined here, 39 species were estimated to occur during the first year and 43 were estimated for the subsequent years (Table 3).

Table 3: Predicted species number that could be detected each year by camera trapping from 2013 to 2017 in Nam Et-Phou Louey National Protected Area, Laos.

	Mean	**SD**	**CI**
Y1	39.20	1.20	37 - 41
Y2	43.00	0.20	43 - 43
Y3	42.80	0.50	42 - 43

Y: year; SD: standard deviation, CI: Bayesian credible interval

4. Discussion

Prompted by hearsay evidence that levels of snaring were unsustainable, and mindful of the national, indeed regional importance of NEPL as a final refuge for both tiger and leopard (Kamler *et al.* 2012; Johnson *et al.* 2016) and important population for dhole (Kamler *et al.* 2012), we conducted the largest camera trapping survey ever attempted in Laos. While we have no counter-factual to judge how much worse things might have been, our results make sadly apparent that the last decade of management interventions has fallen short of the goal of conserving all of the top carnivores: conspicuously, tiger and leopard have been extirpated, and only the dhole persists as the last remaining apex carnivore in the landscape. The Indochinese leopard was not detected during our study, and we conclude it is likely to have been extirpated from the landscape because the last photographs from NEPL were from surveys in 2004 (Rostro-García *et al.* 2016). It appears we recorded the very last tigers, two individuals that had previously been photographed in 2012 (Johnson *et al.* 2016) – it is a chilling realisation that our records in 2013 were the last. That they abruptly disappeared from the survey areas within NEPL after 2013 suggests they were killed, rather than they dispersed from the site or somehow remained undetected in subsequent years. These were the last records of leopard and tiger in Laos. The threatening factors in NEPL are more or less ubiquitous in Laos and it is unlikely that any large, undetected population of either persists anywhere in the country. It seemed the last ten years of conservation management did not prevent tiger and leopard from being extirpated. However, these extirpations were very late in a Lao context, and various other hunting-sensitive species are still doing relatively well in NEPL compared with other Lao PAs.

The extirpation of tigers and leopards in NEPL was likely to have been related to the exponential increase in snaring in NEPL, which occurred despite increases in enforcement activities (Johnson *et al.* 2016). Indiscriminate snaring has been increasing throughout SE Asia during recent years, which is causing a major crisis for biodiversity in the region (Gray *et al.*

2017b). For example, this was likely to have been the main reason for the recent range collapse of leopard in the region (Rostro-García *et al.* 2016). The increase in snaring in NEPL was likely to affect large carnivores such as tiger and leopard more than other species, as also found in Sumatra (Risdianto *et al.* 2016) because large felids are solitary and have naturally low densities. Additionally, large felids have wide ranging movements and thus probably had the largest home ranges of any mammal in the landscape, making them the most susceptible to the increasing numbers of snares, even if snares were primarily set in the buffer zones.

It seems that dhole, along with smaller carnivores, have survived the conditions of the last decade. Nevertheless, we detected 39 mammal species in our survey whereas the survey in 2003 reported 32 (Johnson *et al.* 2006b). We documented the loss of the leopard, but gained two species of macaque (pig-tailed macaque and Rhesus macaque) although at very low probability of initial occupancy, persistence and colonization perhaps explaining their absence in the 2003 survey. With the absence of leopard and tiger within the region, dhole may have prospered as it were detected in all of our survey blocks. Dhole was not detected in one survey block in 2003, the only block in which leopard was detected (Johnson *et al.* 2006b). The records of dhole increased two-fold from the first to the last years of our survey in block 1 (NV) which is also the block that covers almost the whole of survey block 1 of 2003 (Fig. 1). The NV is the block where 90% of the tiger records occurred in 2013. It is tempting to speculate that mesopredator release was involved (Karanth and Sunquist 1995; 2000)

Our findings show that clouded leopard are the most widespread species of carnivore in the NEPL, mirroring the earlier results of Johnson *et al.* (2006b). In contrast, Asian golden cats were the least widespread felid having a mean rate of occupancy (0.37 ± 0.13), which also was similar to that previously reported 0.42 ± 0.14 (Johnson *et al.* 2009). Possible explanations are that the Asian golden cat, but not clouded leopard, have been disadvantaged by the increase in dhole, or either the direct or indirect effects of snaring which, to judge by confiscations, has increased over the last decade (Johnson *et al.* 2016). The Asian golden cat has been reported as

very rare in Nakai - Nam Theun, another protected area in Laos characterised by heavy hunting pressure (Coudrat *et al.* 2014), so this species might be susceptible to snares compared to other meso-felids.

Our results showed that marbled cat and leopard cat have increased since the surveys in 2003 (Johnson *et al*. 2006). These small felids eat mostly rodents (Rajaratnam *et al.* 2007b), of which we detected 10 species, whereas Johnson *et al.* (2006b) detected only four, of which two were species of porcupine. Reasons for differences in detection of rodents between 2003-2004 and 2013-2017 may have been due to differences in camera trap models and sensitivity settings. Interestingly, our detection rate of rodents increased across our three survey periods, which might have been due to the unusually frosty winter at the end of the first survey period. Regardless of whether it was due to changes in rodent numbers, or less susceptibility to snares, the two smallest felid species appeared to have benefited from the last 10 years of management.

Similar to Johnson *et al.* (2006b), we detected 11 other small carnivores in the families Mustelidae, Viverridae, Herpestidae and Prionodontidae , although some of the species differed. For example, we detected the ferret badger(s) *Melogale* complex and binturong *Arctictis binturong*, which were not detected in the previous survey (Johnson *et al.* 2006). In contrast, Johnson *et al.* (2006) detected the striped-back weasel *Mustela strigidorsa* and oriental small-clawed otter *Aonyx cinereus*, which were not detected in our surveys. This guild of Asian carnivores is poorly known (Macdonald *et al.* 2017a). In general, our DCM results suggested an increase in occupancy rate for most species in this group, except for Owston's civet, small Indian civet and spotted linsang *Prionodon pardicolor*.

Sun bear was more widespread in the NEPL than Asian black bear based on our camera-trap survey. In contrast, Scotson (2010) had concluded that sun bear occurred in NEPL at a lower density than black bear based on field sign surveys. This could be true at the time when the previous study was conducted, but it could also be that the signs were recorded opportunistically

and thus did not reflect actual differences in abundance (Scotson 2010). One possibility is that Asian black bear had declined since the survey by Scotson (2010), because this bear species is more prone to capture in snares compared to sun bear, because Asian black bear is more tolerant of human disturbed habitat and is found to wander closer to human settlements (Ngoprasert *et al.* 2011; Garshelis and Steinmetz 2016). In contrast, sun bear is forest dependent species and prefer areas further from humans (Scotson *et al.* 2017). Based on our DCM results, sun bear was more persistent, with a colonisation rate twice that of black bear. However, both bear species are threatened by overhunting for commercial trade for their paws and gall bladders (for traditional Chinese medicine) and habitat loss (Livingstone and Shepherd 2014).

We documented the occurrence of potential prey for large and medium-sized carnivores: red muntjac, stumped-tailed macaque, Eurasian wild pig, silver pheasant, serow and small dark muntjac(s). Reversing the findings of Johnson *et al.* (2006b), we found red muntjac to be much more widespread than stump-tailed macaque. Among large species of potential prey, wild pig was most widespread, followed by serow. Wild pig is overall the most preferred prey of tiger (Hayward *et al*. 2012), and wild pig remained widely distributed in NEPL, indicating tiger population declined due to increases in poaching within NEPL (Johnson *et al*. 2016) rather than prey declines.

The detection probabilities of all four dietary guilds (i.e., carnivore, herbivore, insectivore and omnivore) were similar and low, from which we infer that wildlife of NEPL occurs at low density but seemingly at a higher diversity than in other protected areas in Laos (notwithstanding the loss of tiger and leopard).

5. Conservation implications

We provide a flexible analytical framework for the incorporation of sparse, inconsistent yet valuable data sets on multiple species to assess their status via occupancy as a state process,

offering scope to infer population dynamics over time. This study provides the most recent assessment of animal diversity and status in the NEPL, Laos. Regrettably, the most striking finding is that tiger and leopard have probably been lost from the NEPL, and thus from Laos. This has important implications for tiger conservation planning in Southeast Asia, because NEPL was identified as the last remaining source site for tiger in all of Laos, Cambodia, and Vietnam (Walston *et al.* 2010), thus tiger conservation efforts in the region must now focus on remaining populations in other countries, such as Thailand, Malaysia, Myanmar, and Indonesia (Sumatra). Of the remaining large carnivores in NEPL, clouded leopard and dhole now occupy a priority position. In addition to considering whether the recent extirpation of tiger and leopard can be reversed, attention should focus on the conservation requirements of the clouded leopard and dhole, because both have the potential to act as ambassador species for conservation (*sensu* Macdonald *et al.* 2017b) in NEPL and throughout the country.

Authors' contributions

A.R., conceived the ideas, designed methodology, collected and analysed the data, interpreted analysis results and led the writing of the manuscript. M.K., helped with the design of methodology, interpretation of the analysis results and checking of the manuscript. J.K., D.W.M, supervised the research, checked the manuscript contents and references. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank the Wildlife Conservation Society and the Nam Et- Phou Louey National Protected Area for their extensive in-kind support. We further thank Mr. Phonesouk Chanthalavong for his assistance and Dr. Lucy Talents for her guidance. We deeply grateful for the Exploration Grant from the National Geographic and a grant to DWM from the Robertson Foundation.

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Appendix A

Table A.1. List of species detected and number of observed occupied sites for each species across three survey years during 2013 to 2017 in Nam Et - Phou Louey National Protected Area.

Species (Scientific name)	**Species (Common name)**	**Y1**	**Y2**	**Y3**
Catopuma temminckii	Asian golden cat	49	28	27
Ursus thibetanus	Asian black bear	4	2	5
Atherurus macrourus	Asian brush-tailed porcupine	18	19	20
Macaca assamensis	Assamese macaque	15	7	7
Arctictis binturong	Binturong	4	9	3
Ratufa bicolor	Black giant squirrel	1	3	3
Tamiops complex	Striped squirrel(s)	0	2	0
Neofelis nebulosa	Mainland clouded leopard	41	37	24
Paradoxurus hermaphroditus	Common palm civet	2	48	37
Herpestes urva	Crab-eating mongoose	26	42	33
M. rooseveltorum complex	Small dark muntjac(s)	41	63	60
Cuon alpinus	Dhole	32	17	33
Hystrix brachyura	East Asian porcupine	61	7	35
Sus scrofa	Eurasian wild pig	75	37	32
Melogale complex	Ferret badger(s)	4	2	6

Bos gaurus	Gaur	1	1	0
Polyplectron bicalcaratum	Grey peacock pheasant	13	22	30
Arctonyx collaris	Greater hog badger	62	39	74
Petaurista philippensis	Indian giant flying squirrel	0	0	3
Viverra zibetha	Large Indian civet	48	59	51
Prionailurus bengalensis	Leopard cat	34	43	30
Leopoldamys sabanaus	Long-tailed giant rat	0	17	22
Capricornis milneedwardsii	Indochinese serow	55	42	37
Pardofelis marmorata	Marbled cat	29	27	24
Paguma larvata	Masked palm civet	41	45	44
Macaca leonina	Northern pig-tailed macaque	6	3	6
Chrotogale owstoni	Owston's civet	8	13	25
Rattus exulans	Pacific rat	5	0	18
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	1	4	2
Gallus gallus	Red junglefowl	11	5	31
Muntiacus vaginalis	Northern red muntjac	168	134	106
Dremomys rufigenis	Red-cheeked squirrel	0	14	15
Macaca mulatta	Rhesus macaque	12	5	0
Arborophila rufogularis	Rufous-throated partridge	0	7	20
Cervus unicolor	Sambar	24	14	9
Lophura nycthemera	Silver pheasant	50	37	47

Viverricula indica	Small Indian civet	2	4	9
Prionodon pardicolor	Spotted linsang	6	7	15
Macaca arctoides	Stump-tailed macaque	105	49	87
Helarctos malayanus	Sun bear	28	47	29
Panthera tigris	Tiger	14	0	0
Rattus nitidus	White-footed Indochinese rat	0	5	0
Martes flavigula	Yellow-throated marten	77	69	65

Table A.2. Estimated mean initial occupancy probabilities (psi1) of species detected in Nam Et - Phou Louey National Protected Area during 2013 - 2017

Species (Scientific name)	**Species (Common name)**	**psi1**	**sd**	**CrI**
Catopuma temminckii	Asian golden cat	0.371	0.128	0.122 - 0.631
Ursus thibetanus	Asian black bear	0.090	0.105	0 - 0.289
Atherurus macrourus	Asian brush-tailed porcupine	0.074	0.032	0.019 - 0.129
Macaca assamensis	Assamese macaque	0.096	0.071	0.002 - 0.224
Arctictis binturong	Binturong	0.101	0.095	0.004 - 0.29
Ratufa bicolor	Black giant squirrel	0.013	0.017	0 - 0.04
Tamiops complex	Striped squirrel(s)	0.006	0.012	0 - 0.021
Neofelis nebulosa	Mainland clouded leopard	0.512	0.176	0.181 - 0.875
Paradoxurus hermaphroditus	Common palm civet	0.015	0.023	0 - 0.043
Herpestes urva	Crab-eating mongoose	0.121	0.100	0.002 - 0.313
M. rooseveltorum complex	Small dark muntjac(s)	0.156	0.101	0.006 - 0.346
Cuon alpinus	Dhole	0.386	0.144	0.128 - 0.69
Hystrix brachyura	East Asian porcupine	0.286	0.067	0.15 - 0.417
Sus scrofa	Eurasian wild pig	0.428	0.120	0.178 - 0.665
Melogale complex	Ferret badger(s)	0.041	0.037	0.001 - 0.107
Bos gaurus	Gaur	0.027	0.051	0 - 0.095
Polyplectron bicalcaratum	Grey peacock pheasant	0.072	0.065	0.001 - 0.186
Arctonyx collaris	Greater hog badger	0.297	0.130	0.061 - 0.559

Petaurista philippensis	Indian giant flying squirrel	0.007	0.015	0 - 0.028
Viverra zibetha	Large Indian civet	0.237	0.076	0.082 - 0.382
Prionailurus bengalensis	Leopard cat	0.204	0.088	0.04 - 0.374
Leopoldamys sabanaus	Long-tailed giant rat	0.005	0.013	0 - 0.017
Capricornis milneedwardsii	Indochinese serow	0.317	0.147	0.035 - 0.596
Pardofelis marmorata	Marbled cat	0.228	0.128	0.023 - 0.481
Paguma larvata	Masked palm civet	0.238	0.135	0.016 - 0.496
Macaca leonina	Northern pig-tailed macaque	0.058	0.071	0 - 0.185
Chrotogale owstoni	Owston's civet	0.025	0.030	0 - 0.07
Rattus exulans	Pacific rat	0.027	0.030	0 - 0.075
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.025	0.036	0 - 0.083
Gallus gallus	Red junglefowl	0.097	0.081	0.002 - 0.247
Muntiacus vaginalis	Northern red muntjac	0.684	0.071	0.553 - 0.817
Dremomys rufigenis	Red-cheeked squirrel	0.005	0.009	0 - 0.017
Macaca mulatta	Rhesus macaque	0.079	0.040	0.017 - 0.15
Arborophila rufogularis	Rufous-throated partridge	0.005	0.011	0 - 0.018
Cervus unicolor	Sambar	0.108	0.039	0.038 - 0.183
Lophura nycthemera	Silver pheasant	0.329	0.116	0.103 - 0.568
Viverricula indica	Small Indian civet	0.019	0.020	0 - 0.052
Prionodon pardicolor	Spotted linsang	0.059	0.041	0.004 - 0.132
Macaca arctoides	Stump-tailed macaque	0.558	0.099	0.349 - 0.76

Helarctos malayanus	Sun bear	0.178	0.075	0.043 - 0.321
Panthera tigris	Tiger	0.202	0.212	0.001 - 0.711
Rattus nitidus	White-footed Indochinese rat	0.005	0.011	0 - 0.015
Martes flavigula	Yellow-throated marten	0.332	0.075	0.173 - 0.481

Table A.3. Estimated mean persistence probabilities (phi) of species detected in Nam Et - Phou Louey National Protected Area during 2013 - 2017

Species (Scientific name)	Species (Common name)	phi	sd	CrI
Catopuma temminckii	Asian golden cat	0.430	0.106	0.23 - 0.636
Ursus thibetanus	Asian black bear	0.315	0.174	0.032 - 0.659
Atherurus macrourus	Asian brush-tailed porcupine	0.317	0.085	0.161 - 0.486
Macaca assamensis	Assamese macaque	0.349	0.121	0.121 - 0.581
Arctictis binturong	Binturong	0.308	0.167	0.042 - 0.643
Ratufa bicolor	Black giant squirrel	0.382	0.159	0.098 - 0.696
Tamiops complex	Striped squirrel(s)	0.313	0.158	0.034 - 0.615
Neofelis nebulosa	Mainland clouded leopard	0.538	0.130	0.29 - 0.789
Paradoxurus hermaphroditus	Common palm civet	0.275	0.078	0.128 - 0.427
Herpestes urva	Crab-eating mongoose	0.330	0.087	0.171 - 0.505
M. rooseveltorum complex	Small dark muntjac(s)	0.535	0.065	0.408 - 0.661
Cuon alpinus	Dhole	0.306	0.135	0.077 - 0.575
Hystrix brachyura	East Asian porcupine	0.152	0.053	0.059 - 0.258
Sus scrofa	Eurasian wild pig	0.309	0.069	0.177 - 0.444
Melogale complex	Ferret badger(s)	0.294	0.145	0.049 - 0.582
Bos gaurus	Gaur	0.331	0.161	0.052 - 0.645
Polyplectron bicalcaratum	Grey peacock pheasant	0.509	0.134	0.251 - 0.764
Arctonyx collaris	Greater hog badger	0.513	0.072	0.37 - 0.651

Petaurista philippensis	Indian giant flying squirrel	0.379	0.178	0.062 - 0.721
Viverra zibetha	Large Indian civet	0.379	0.063	0.261 - 0.506
Prionailurus bengalensis	Leopard cat	0.372	0.079	0.22 - 0.529
Leopoldamys sabanaus	Long-tailed giant rat	0.423	0.128	0.194 - 0.688
Capricornis milneedwardsii	Indochinese serow	0.452	0.071	0.311 - 0.589
Pardofelis marmorata	Marbled cat	0.304	0.100	0.126 - 0.507
Paguma larvata	Masked palm civet	0.388	0.084	0.232 - 0.558
Macaca leonina	Northern pig-tailed macaque	0.330	0.162	0.044 - 0.642
Chrotogale owstoni	Owston's civet	0.132	0.074	0.013 - 0.275
Rattus exulans	Pacific rat	0.286	0.133	0.056 - 0.554
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.394	0.166	0.107 - 0.73
Gallus gallus	Red junglefowl	0.675	0.164	0.355 - 0.962
Muntiacus vaginalis	Northern red muntjac	0.708	0.036	0.637 - 0.778
Dremomys rufigenis	Red-cheeked squirrel	0.266	0.122	0.052 - 0.504
Macaca mulatta	Rhesus macaque	0.334	0.123	0.100 - 0.57
Arborophila rufogularis	Rufous-throated partridge	0.564	0.182	0.215 - 0.897
Cervus unicolor	Sambar	0.311	0.082	0.151 - 0.469
Lophura nycthemera	Silver pheasant	0.540	0.109	0.333 - 0.756
Viverricula indica	Small Indian civet	0.391	0.162	0.093 - 0.699
Prionodon pardicolor	Spotted linsang	0.354	0.148	0.092 - 0.652

Macaca arctoides	Stump-tailed macaque	0.431	0.054	0.329 - 0.539
Helarctos malayanus	Sun bear	0.439	0.090	0.267 - 0.617
Panthera tigris	Tiger	0.155	0.081	0.023 - 0.315
Rattus nitidus	White-footed Indochinese rat	0.208	0.120	0.015 - 0.44
Martes flavigula	Yellow-throated marten	0.529	0.056	0.419 - 0.641

Table A.4. Estimated mean colonization probabilities (gamma) of species detected in Nam Et - Phou Louey National Protected Area during 2013 - 2017

Species (Scientific name)	Species (Common name)	gamma	sd	CrI
Catopuma temminckii	Asian golden cat	0.242	0.065	0.127 - 0.374
Ursus thibetanus	Asian black bear	0.136	0.128	0.013 - 0.405
Atherurus macrourus	Asian brush-tailed porcupine	0.090	0.016	0.059 - 0.122
Macaca assamensis	Assamese macaque	0.049	0.019	0.016 - 0.085
Arctictis binturong	Binturong	0.207	0.188	0.01 - 0.664
Ratufa bicolor	Black giant squirrel	0.029	0.017	0.005 - 0.062
Tamiops complex	Striped squirrel(s)	0.016	0.012	0.001 - 0.039
Neofelis nebulosa	Mainland clouded leopard	0.507	0.165	0.23 - 0.871
Paradoxurus hermaphroditus	Common palm civet	0.305	0.039	0.228 - 0.38
Herpestes urva	Crab-eating mongoose	0.349	0.063	0.232 - 0.472
M. rooseveltorum complex	Small dark muntjac(s)	0.378	0.045	0.291 - 0.466
Cuon alpinus	Dhole	0.451	0.154	0.209 - 0.786
Hystrix brachyura	East Asian porcupine	0.142	0.024	0.095 - 0.19
Sus scrofa	Eurasian wild pig	0.290	0.055	0.187 - 0.4
Melogale complex	Ferret badger(s)	0.055	0.030	0.013 - 0.11
Bos gaurus	Gaur	0.024	0.040	0 - 0.079
Polyplectron bicalcaratum	Grey peacock pheasant	0.174	0.030	0.119 - 0.234
Arctonyx collaris	Greater greater hog badger	0.343	0.041	0.263 - 0.423

Petaurista philippensis	Indian giant flying squirrel	0.033	0.031	0.002 - 0.088
Viverra zibetha	Large Indian civet	0.373	0.045	0.286 - 0.463
Prionailurus bengalensis	Leopard cat	0.304	0.053	0.202 - 0.408
Leopoldamys sabanaus	Long-tailed giant rat	0.134	0.024	0.088 - 0.182
Capricornis milneedwardsii	Indochinese serow	0.282	0.050	0.186 - 0.382
Pardofelis marmorata	Marbled cat	0.342	0.107	0.168 - 0.554
Paguma larvata	Masked palm civet	0.451	0.084	0.307 - 0.627
Macaca leonina	Northern pig-tailed macaque	0.078	0.061	0.011 - 0.177
Chrotogale owstoni	Owston's civet	0.123	0.020	0.085 - 0.164
Rattus exulans	Pacific rat	0.086	0.024	0.043 - 0.132
Callosciurus sp.	Pallas's and/or Inornate Squirrel	0.063	0.061	0.003 - 0.173
Gallus gallus	Red junglefowl	0.189	0.045	0.11 - 0.277
Muntiacus muntjak	Red muntjac	0.605	0.066	0.477 - 0.735
Dremomys rufigenis	Red-cheeked squirrel	0.127	0.032	0.069 - 0.187
Macaca mulatta	Rhesus macaque	0.012	0.008	0 - 0.027
Arborophila rufogularis	Rufous-throated partridge	0.096	0.022	0.057 - 0.141
Cervus unicolor	Sambar	0.048	0.014	0.023 - 0.075
Lophura nycthemera	Silver pheasant	0.355	0.069	0.231 - 0.495
Viverricula indica	Small Indian civet	0.059	0.020	0.023 - 0.097
Prionodon pardicolor	Spotted Linsang	0.133	0.047	0.057 - 0.224
Macaca arctoides	Stump-tailed macaque	0.588	0.057	0.478 - 0.704

Helarctos malayanus	Sun bear	0.314	0.060	0.209 - 0.436
Panthera tigris	Tiger	0.023	0.029	0 - 0.072
Rattus nitidus	White-footed Indochinese rat	0.022	0.010	0.005 - 0.041
Martes flavigula	Yellow-throated marten	0.351	0.041	0.272 - 0.43

Table A.5. Estimated mean detection probabilities (p) of species detected in Nam Et - Phou Louey National Protected Area during 2013 - 2017

Species (Scientific name)	Species (Common name)	p	sd	CrI
Catopuma temminckii	Asian golden cat	0.116	0.026	0.067 - 0.167
Ursus thibetanus	Asian black bear	0.102	0.065	0.011 - 0.231
Atherurus macrourus	Asian brush-tailed porcupine	0.288	0.092	0.109 - 0.444
Macaca assamensis	Assamese macaque	0.146	0.043	0.063 - 0.23
Arctictis binturong	Binturong	0.064	0.037	0.011 - 0.136
Ratufa bicolor	Black giant squirrel	0.144	0.065	0.032 - 0.269
Tamiops complex	Striped squirrel(s)	0.176	0.093	0.026 - 0.36
Neofelis nebulosa	Mainland clouded leopard	0.074	0.025	0.033 - 0.119
Paradoxurus hermaphroditus	Common palm civet	0.217	0.043	0.122 - 0.296
Herpestes urva	Crab-eating mongoose	0.146	0.042	0.067 - 0.226
M. rooseveltorum complex	Small dark muntjac(s)	0.188	0.062	0.072 - 0.309
Cuon alpinus	Dhole	0.085	0.031	0.032 - 0.145
Hystrix brachyura	East Asian porcupine	0.229	0.058	0.114 - 0.343
Sus scrofa	Eurasian wild pig	0.162	0.034	0.094 - 0.224
Melogale complex	Ferret badger(s)	0.111	0.048	0.029 - 0.206
Bos gaurus	Gaur	0.117	0.07	0.01 - 0.252
Polyplectron bicalcaratum	Grey peacock pheasant	0.181	0.047	0.086 - 0.268
Arctonyx collaris	Greater hog badger	0.193	0.053	0.088 - 0.295
Petaurista philippensis	Indian giant flying squirrel	0.133	0.073	0.016 - 0.274

Viverra zibetha	Large Indian civet	0.183	0.066	0.061 - 0.307
Prionailurus bengalensis	Leopard cat	0.152	0.035	0.08 - 0.221
Leopoldamys sabanaus	Long-tailed giant rat	0.196	0.087	0.051 - 0.371
Capricornis milneedwardsii	Indochinese serow	0.164	0.054	0.069 - 0.275
Pardofelis marmorata	Marbled cat	0.106	0.028	0.056 - 0.16
Paguma larvata	Masked palm civet	0.138	0.035	0.071 - 0.21
Macaca leonina	Northern pig-tailed macaque	0.091	0.045	0.016 - 0.179
Chrotogale owstoni	Owston's civet	0.274	0.067	0.122 - 0.393
Rattus exulans	Pacific rat	0.155	0.068	0.037 - 0.291
Callosciurus erythraeus and/or *C. inornatus*	Pallas's and/or Inornate Squirrel	0.109	0.062	0.014 - 0.23
Gallus gallus	Red junglefowl	0.117	0.05	0.038 - 0.214
Muntiacus vaginalis	Northern red muntjac	0.306	0.056	0.179 - 0.403
Dremomys rufigenis	Red-cheeked squirrel	0.174	0.063	0.06 - 0.297
Macaca mulatta	Rhesus macaque	0.168	0.054	0.066 - 0.273
Arborophila rufogularis	Rufous-throated partridge	0.196	0.061	0.083 - 0.317
Cervus unicolor	Sambar	0.242	0.073	0.102 - 0.378
Lophura nycthemera	Silver pheasant	0.14	0.027	0.088 - 0.193
Viverricula indica	Small Indian civet	0.129	0.059	0.031 - 0.245
Prionodon pardicolor	Spotted linsang	0.103	0.037	0.039 - 0.175
Macaca arctoides	Stump-tailed macaque	0.19	0.067	0.068 - 0.324
Helarctos malayanus	Sun bear	0.148	0.04	0.075 - 0.227

Panthera tigris	Tiger	0.083	0.045	0.009 - 0.169
Rattus nitidus	White-footed Indochinese rat	0.223	0.1	0.047 - 0.418
Martes flavigula	Yellow-throated marten	0.244	0.067	0.099 - 0.361

R-BUGS Script A.1. Dynamic community model

```
#############################################################################
############ Dynamic community model: Random Species Effects ##############
# Making all four parameters guild-dependent (i.e. psi1, phi, gamma, & p ##
#############################################################################
### This model will:
# Estimate overall psi, p for each species
# Estimate psi per year per species
# Estimate psi1, p, phi, gamma of guild groups
# Estimate overall richness by size/guild/year; by guild/year; and point/guild

#We assume that guild affects the mean of the parameter for a species,
#but that it does not affect the heterogeneity among species.
#That is, instead of fitting a single Normal distribution for each parameter type (to represent the species-by-species variability in psi1, phi, gamma or p), we now estimate 4 such Normal distributions for each, where the mean of the four is different, but the variance (spread) is identical.

library(jagsUI)
library(wiqid)
library(reshape)

# Read in data set
str(dat <- read.csv("DH_spc.csv", header = TRUE, sep = ',', na.string = '-') )

# Get list and sample size for all 4 dimensions
nsite <- length(unique(dat$station)))     #300 sites in total for 4 blocks
(site.list <- unique(dat$station))        # Getting unique site ID
(nrepmax <- 5)                                    # Total occasion per season
(nyear <- 3)                                    # number of year
(year <- 1:3)                                     # vector of years (1, 2, 3)
(nspec <- length(unique(levels(dat$species))))          # Total number of species
(specnames <- levels(dat$species))                # Getting species name
################################################
###### Format detection data into a 4d array ###
################################################
Y <- array(NA, dim = c(nsite, nrepmax, nyear, nspec))
dimnames(Y) <- list(site.list, 1:5, 1:3, specnames)

for(t in 1:3){              #Loop over 3 years
  for(s in 1:43){                #Lopp over 43 species
    sel.rows <- which((dat$year == t & dat$species == specnames[s]))
    Y[1:300, 1:5, t, s] <- as.matrix(dat[sel.rows,4:8])
  } }

# Do a quick sum test
sum(Y, na.rm = TRUE)  ;   sum(dat[,4:8] , na.rm = TRUE)

# get detection frequencies by summing over 2nd dimension
str(Y2 <- apply(Y, c(1,3,4), sum, na.rm = TRUE))

### Since the missing value patterns are not identical everywhere,
### we need to get the number of active occasions for each site, year and species, too.

# get binomial trial size (nrep)
str(nrep <- apply(Y, c(1,3,4), function(x) sum(!is.na(x))))

# Histogram of these detection frequencies
hist(Y2, col = 'grey', main = "Detection Frequencies")

# Histogram of nreps
```

```
hist(nrep, col = 'grey', main = "Active occasions")

# Compute some statistics, for instance number of observed occupied sites for a species
tmp <- Y2               # Make a copy
tmp[tmp > 1] <- 1
nocc.obs <- apply(tmp, c(2,3), sum, na.rm = TRUE)

##############################
# For this, we need the membership of each point to the guild and add this as a covariate.
# We have to use numbers, which correspond to these levels in this order: Carnivore Herbivore Insectivore
Omnivore

# Create block covariate (N)
block <- as.numeric(dat$block[1:300])
table(block)

# Create guild covariate
(tmp <- aggregate(as.numeric(dat$diet), by = list(dat$species), FUN = mean))
guild <- tmp$x
table(guild)

# Bundle and summarize data set
str(bdata <- list(y = Y2, nrep = nrep, nsite = dim(Y2)[1], nyear = 3, nspec = dim(Y2)[3], block = block, guild =
guild))

############################################################
########### Specify model in BUGS language ##############
############################################################

sink("DCM.txt")
cat("model {

# Specify priors and hyperpriors
# Model for initial occupancy (has a block effect)
# Also has a guild effect
for(k in 1:nspec){
  for (i in 1:nsite){          # Loop over sites
    logit(psi1[i, k]) <- lpsi1[k] + lpsi1.block[block[i], k]
            }
    lpsi1[k] ~ dnorm(mu.lpsi1[guild[k]], tau.lpsi1)
}

for(g in 1:4){     # Now have mean dependent on guild
  mu.lpsi1[g] <- logit(mean.psi1[g])    # Initial occupancy per guild
  mean.psi1[g] ~ dunif(0, 1)
}
tau.lpsi1 <- pow(sd.lpsi1, -2)    # Note spread of species NOT guild-dep
sd.lpsi1 ~ dunif(0, 30)

# Add random block effect in initial occupancy
for(k in 1:nspec){
  for (b in 1:4){          # Loop over blocks
    lpsi1.block[b, k] ~ dnorm(0, tau.lpsi1.block[k])
  }
  tau.lpsi1.block[k] <- pow(sd.lpsi1.block[k], -2)
  sd.lpsi1.block[k] ~ dnorm(0, 0.5)I(0,)

# Models for persistence and colonization
# Both have now an effect of guild
for(k in 1:nspec){
  logit(phi[k]) <- lphi[k]      # Persistence
  lphi[k] ~ dnorm(mu.lphi[guild[k]], tau.lphi)
```

```
  logit(gamma[k]) <- lgamma[k]  # Colonization
  lgamma[k] ~ dnorm(mu.lgamma[guild[k]], tau.lgamma)
}

for(g in 1:4){     # Now have mean dependent on guild
  mu.lphi[g] <- logit(mean.phi[g])      # Persistence
  mean.phi[g] ~ dunif(0, 1)
}
tau.lphi <- pow(sd.lphi, -2)    # Note spread of species NOT guild-dep
sd.lphi ~ dunif(0, 30)

for(g in 1:4){     # Now have mean dependent on guild
  mu.lgamma[g] <- logit(mean.gamma[g])      # Colonization
  mean.gamma[g] ~ dunif(0, 1)
}
tau.lgamma <- pow(sd.lgamma, -2)  # Note spread of species NOT guild-dep
sd.lgamma ~ dunif(0, 30)


# Models for detection (has a block effect – average over years)
# Also has a guild effect

for(k in 1:nspec){
  for (i in 1:nsite){          # Loop over sites
    logit(p[i,k]) <- lp[k] + lp.block[block[i], k]
  }
  lp[k] ~ dnorm(mu.lp[guild[k]], tau.lp)
}

for(g in 1:4){     # The mean is now dependent on guild
  mu.lp[g] <- logit(mean.p[g])    # Mean detection per guild
  mean.p[g] ~ dunif(0, 1)
}
tau.lp <- pow(sd.lp, -2)    # Note spread of species NOT guild-dep
sd.lp ~ dunif(0, 30)

# Add random block effect in detection (same for all years)
for(k in 1:nspec){
  for (b in 1:4){          # Loop over blocks
    lp.block[b, k] ~ dnorm(0, tau.lp.block[k])
  }
  tau.lp.block[k] <- pow(sd.lp.block[k], -2)
  sd.lp.block[k] ~ dnorm(0, 0.5)I(0,)
}

# Ecological submodel: Define state conditional on parameters
for (i in 1:nsite){          # Loop over sites
  for(k in 1:nspec){         # Loop over species

    # Initial conditions of system
    z[i,1, k] ~ dbern(psi1[i,k])  # Presence/absence at start of study

    # State transitions
    for (t in 2:nyear){       # Loop over years
      z[i,t,k] ~ dbern(z[i,t-1,k] * phi[k] + (1-z[i,t-1, k]) * gamma[k])
    } }}

# Observation model
for (i in 1:nsite){
  for(k in 1:nspec){
    for (t in 1:nyear){
```

```
    y[i,t,k] ~ dbin(z[i,t,k] * p[i,k], nrep[i,t,k])

        #Create simulated data set to calculate the bayesian p-value

        ynew[i,t,k] ~ dbin(z[i,t,k] * p[i,k], nrep[i,t,k])

        # Pearson residuals
d[i,t,k] <- (y[i,t,k] - z[i,t,k] * p[i,k] * nrep[i,t,k]) / sqrt(nrep[i,t,k] * z[i,t,k] * p[i,k] * (1 - z[i,t,k]) + 0.001)
dnew[i,t,k] <- (ynew[i,t,k] - z[i,t,k] * p[i,k] * nrep[i,t,k]) / sqrt(nrep[i,t,k] * z[i,t,k] * p[i,k] * (1 - z[i,t,k]) + 0.001)
        d2[i,t,k] <- pow(d[i,t,k], 2)
        dnew2[i,t,k] <- pow(dnew[i,t,k], 2)
        } }}

# Derived parameters: Number and proportion of occupied sites
for(k in 1:nspec){
  n.occ[1, k] <- sum(z[,1,k])   # Number of occupied sites
  psi.fs[1, k] <- n.occ[1, k]/300  # Finite sample occupancy proportion
  for (t in 2:nyear){
    n.occ[t, k] <- sum(z[,t,k]) # Number of occupied sites
    psi.fs[t, k] <- n.occ[t,k]/300  # Finite sample occupancy proportion
  }
}

# Derived parameters: Mean occupancy and detection per species
for(k in 1:nspec){
  species.mean.psi1[k] <- ilogit(lpsi1[k])
  species.mean.p[k] <- ilogit(lp[k])
#  mean.psi1[k] <- 1 / (1 + exp(-lpsi1[k]))
#  mean.p[k] <- 1 / (1 + exp(-lp[k]))
}

# Calculate the discrepancy measure
  p.fit <- sum(d2[1: nsite, 1: nyear, 1:nspec])
  p.fitnew <- sum(dnew2[1: nsite, 1: nyear, 1:nspec])
}
",fill = TRUE)
sink()

# Initial values
zobs <- Y2
zobs[zobs > 1] <- 1            # Observed occurrence as inits for z
inits <- function(){list(z = zobs)}

# Parameters monitored
params <- c("mu.lpsi1", "mean.psi1", "sd.lpsi1", “sd.lpsi1.block", "mu.lphi", "mean.phi", "sd.lphi",
"mu.lgamma", "mean.gamma", "sd.lgamma", "mu.lp", "mean.p", "sd.lp", "phi", "gamma", "species.mean.psi1",
"species.mean.p", "sd.lp.block", "n.occ", "psi.fs", "z", "p.fit", p.fitnew")

# MCMC settings

ni <- 100000  ;  nt <- 10  ;  nb <- 50000  ;  nc <- 3    # 16 hours    # This provide 3 * (100000 - 50000)/10 =
15000 samples
# Run the model
out <- jags(bdata, inits, params, "DCM.txt", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, parallel =
TRUE)

par(mfrow = c(3,3))  ;  traceplot(out)

#Save the results into a file for later
save(out, file="DCM_100k_iter.Rdata")
```

Chapter 3

Density Trends of Small and Meso-Felids in Nam Et - Phou Louey National Protected Area, Lao PDR

Submitted to *Journal of Mammalogy*

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Abstract

Determining trends in the densities of a guild of species can help illuminate their interactions, and the impacts that humans might have on them. Of the four species of non-pantherine felids found in Nam Et - Phou Louey National Protected Area (NEPL), Lao PDR, three felids (clouded leopard *Neofelis nebulosa*, leopard cat *Prionailurus bengalensis* and marbled cat *Pardofelis marmorata*) are individually identifiable from their pelage markings, making it possible to estimate their population densities via camera trapping and spatial capture-recapture models. Using data from three camera trap surveys from 2013 to 2017, we assessed population density trends of these species. Mean (± *SD*) density estimates for all years were 1.77 ± 0.30 individuals/100 km^2 for clouded leopard, 1.50 ± 0.30 individuals/100 km^2 for leopard cat, and 3.80 ± 0.70 individuals/100 km^2 for marbled cat. There was a declining trend in density across the study years for all three species, with a stronger rate of decline for clouded leopard and leopard cat. There was no evidence that mesopredator release occurred as a result of tiger (*Panthera tigris*) and leopard (*P. pardus*) extirpations. We believe that snaring, the factor that led to the extirpation of tigers and leopards in NEPL, is now contributing to the decline of smaller felids, to an extent that over-rides any potential effects of mesopredator release on their densities and interactions. We recommend increased efforts to remove snares and a more effective enforcement regime in NEPL, along with better engagement and education of local people to prevent setting of snares. These actions might be the only hope for saving the remaining members of the felid guild in NEPL.

***Key words*:** camera traps, clouded leopard, density, felids, Laos, leopard cat, marbled cat, Nam Et - Phou Louey, snaring, spatial capture-recapture.

Introduction

The population densities of members of an ecological guild might help resolve aspects of the competitive dynamics within the guild, bearing in mind competition amongst sympatric species with similar niches (Case and Gilpin 1974). These interactions are of fundamental interest in community ecology, and highly relevant to conservation (Karanth *et al.* 2006; Obbard *et al.* 2010; Kery *et al.* 2011). Guilds of felids are particularly noteworthy in provoking questions about co-existence and niche theory, and because they are often threatened.

IUCN range maps indicate that there are 8 species of wild felid in countries throughout mainland Southeast Asia (e.g. Burnham *et al.* 2012; Macdonald *et al.* 2012), many of which are threatened (e.g. Dickman *et al.* 2015). All eight species are found in Laos, making it a priority country for both the study and conservation of felids. Furthermore, recent range-wide analyses of clouded leopard (*Neofelis nebulosa*) distribution suggest that Laos, along with Myanmar, constitute the main population refuges for this species across Southeast Asia (Macdonald *et al.* submitted). With 6 species of felids, the Nam Et - Phou Louey National Protected Area (hereafter NEPL) in Laos PDR is home to the most diverse hyper-carnivore communities in the Indochinese region. Despite this, the only carnivore density study available for this area was for tiger in 2006 (Johnson *et al.* 2006b). Therefore, more data are needed for other carnivore species, to determine their baselines densities, trends in densities, interspecific interactions, and impacts by humans.

This study aims to estimate density trends of the meso- and small felids with unique pelage markings in NEPL: the clouded leopard, the marbled cat (*Pardofelis marmorata*), and the leopard cat (*Prionailurus bengalensis)*. The clouded leopard is a meso-felid (12-23 kg) listed as Vulnerable by the IUCN (Grassman *et al.* 2016a). This species is thought to be particularly arboreal and has an extremely long tail to aid in balancing, making it one of the best climbers in the felid family (Grassman *et al.* 2016a). Its diet consists of small- and medium-sized ungulates as well as primates, porcupines, squirrels, and pheasants (Grassman *et al.* 2005a). Its

population is rapidly declining across its range (Hunter *et al.* 2011; D'Cruze and Macdonald 2015; Grassman *et al.* 2016a). The main causes of the decline include hunting, habitat fragmentation, and habitat degradation (Nowell 2007; Oswell 2010). Previous studies have estimated the density of clouded leopard in India, Malaysia, Myanmar and Bhutan (Borah *et al.* 2013; Mohamad *et al.* 2015; Naing *et al.* 2017; Singh and Macdonald 2017; Penjor *et al.* 2018). Among these studies, clouded leopard density estimate from the Dampa Wildlife Reserve, India (Singh and Macdonald 2017), was the highest which thought to be due the local extirpation, or very low density of tiger (*Panthera tigris*) and leopard (*Panthera pardus*).

The Leopard cat is a small felid (3-7 kg) that is relatively common throughout its range, listed as Least Concern by the IUCN (Ross *et al.* 2015). The species is more of a habitat generalist and its diet consists of squirrels, small rodents and birds (Ross *et al.* 2015). Its population is thought to be stable despite the main threat to its population being exploitation for trade (Ross *et al.* 2015). Previous studies have estimated the density of this species in India and Malaysia (Bashir *et al.* 2013; Mohamed *et al.* 2013b; Selvan *et al.* 2014; Srivathsa *et al.* 2015; Chua *et al.* 2016). Based on the comparison of findings from these studies, the leopard cat density estimate reported by Bashir *et al.* (2013) was the highest which could be tributed to the area's remoteness and topography of a sharp elevation gradient (from 1,220 to 8,586 m a.s.l.).

The marbled cat is another small felid (2-4 kg) with a wide distribution range, although it is listed as Near Threatened by the IUCN (Ross *et al.* 2016). It has a uniquely marbled coat pattern with a big, fluffy and long tail for counter balancing when climbing. The diet of this species is thought to be birds and rodents, including squirrels (Ross *et al.* 2016). Unlike the leopard cat, the marbled cat populations are thought to be declining across its range (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Ross *et al.* 2016). Previous studies have estimated the density of marbled cat in Malaysia, Myanmar, and India (Hearn *et al.* 2016b; Naing *et al.* 2017; Singh and Macdonald 2017). Findings from these previous studies showed that relatively high density estimates of the marbled cat are from areas with low-level of human disturbances

(Hearn *et al.* 2016b; Naing *et al.* 2017). Here, we provide additional estimates of the population densities of these three species.

In NEPL, leopard was recently extirpated, with the last photograph recorded in 2004 (Rostro-García *et al.* 2016). Tiger numbers in NEPL declined from 2004 to 2012, when only two identifiable individuals remained (Johnson *et al.* 2016). During the first year of this study, the same two tigers were photographed on several occasions, however neither was photographed during the final three years of the study. We conclude that tiger probably became extirpated in NEPL in 2014. Johnson et al. (2016) showed that the tiger decline in NEPL was caused by an exponential increase in snaring, which occurred despite increases in ranger patrols and gun confiscations. Following the extirpations of tiger and leopard, the largest felid remaining in NEPL is the clouded leopard. Assuming strong interference competition between felid species in Asia, the mesopredator release hypothesis (Soulé *et al.* 1988) would predict that clouded leopard numbers should increase in the absence of tiger and leopard. Tiger is known to kill and displace leopard (Seidensticker 1976; McDougal 1988; Odden and Wegge 2009), and consequently leopard numbers decrease with increasing tiger numbers (Harihar *et al.* 2011; Mondal *et al.* 2012). Additionally, tiger reportedly predate on several species of smaller carnivores in Southeast Asia (Simcharoen *et al.* 2018), thus tiger potentially could predate on clouded leopard and other smaller felids as well. Similarly, leopards commonly predate on smaller carnivores in Southeast Asia (Grassman 1999; Rostro-García *et al.* 2018; Simcharoen *et al.* 2018). Consequently, clouded leopard might benefit from the absence of tiger and leopard. In turn, higher numbers of clouded leopard might suppress populations of small felids such as marbled cat and leopard cat (Macdonald *et al.* 2010b). A similar relationship occurs among large, medium, and small canids (Macdonald and Sillero-Zubiri 2004), as for example coyote (*Canis latrans*) numbers increase in the absence of wolve (*C. lupus*) due to mesopredator

release, and in turn red fox (*Vulpes vulpes*) numbers decrease in response to increased numbers of coyote (Levi and Wilmers 2012).

The goal of this study is to determine the density trend of clouded leopard, marbled cat, and leopard cat in NEPL, and to examine if either mesopredator release or poaching is affecting their densities and interactions. In short, from the mesopredator release hypothesis we predict that clouded leopard densities will increase following the extirpation of tiger during the first year of the study. If that prediction is fulfilled, we predict that densities of marbled cat and leopard cat will decrease during the study due to the increasing numbers of clouded leopard. Alternatively, if indiscriminate snaring continued to increase during the study, then we predict that numbers of all three felid species would decrease during the study. Clouded leopard is Threatened and marbled cat is Near Threatened, so determining which factors most influence their densities will help inform conservation efforts in NEPL and throughout the region. Finally, we also conducted a literature review of previous density estimates for these three cat species, so that our density estimates could be put in context of the entire species' ranges.

Materials and Methods

Study site.— The NEPL is located in the northern highlands of Lao PDR (between latitude 19°50' - 20°50'N and longitude 103°00' - 103°53'E), bordering Vietnam along its northern boundary (Fig.1). It spans 5,969 km^2 of mountainous terrain across seven districts and three provinces (Houaphan, Luang Prabang, and Xiengkhuang). The topography of NEPL is rugged, with elevation ranging from 400 - 2257 m, of which >60% is above 1000 m and 91% with slopes >12% (Johnson 2012). Vegetation is largely dominated by dry evergreen and semi-evergreen forests. However, around one-third of the park is degraded forest with a canopy cover of less than 20%. The climate in Laos is tropical monsoonal with a rainy season lasting from May to October followed by a distinct dry season for the remainder of the year (Duckworth *et al.* 1999a). Annual rainfall ranges from 1400 to 1800 mm (Johnson 2012). The NEPL is divided

into two protected zones; a totally protected core zone where human access is prohibited and a peripheral managed use zone (Fig.1).

Camera trapping.—We used systematic camera trap surveys to estimates densities of three felid species in the NEPL. This non-invasive technique has been used widely to study elusive carnivore species at low densities (Karanth and Nichols 1998; Datta *et al.* 2008; McCarthy *et al.* 2008; Balme *et al.* 2009; O'Brien 2011; Bernard *et al.* 2013; Hearn *et al.* 2013; Rostro-García *et al.* 2018). Our camera trap surveys were carried out in four ~200 km^2 blocks within the NEPL NPA core zone: Nam Poung - Na Vaen (NPNV – block 1); Pha Daeng (PD – block 2); Phoupha - Siphou (PS – block 3) and Nam Neun (NN – block 4) (Fig.1). In 2013 we surveyed all four blocks while the repeated surveys of 2015/16 and 2016/17 only covered three blocks (i.e., NPNV, PD and PS) due to limited resources. Therefore, for the purpose of consistency, here we only used data from those three blocks.

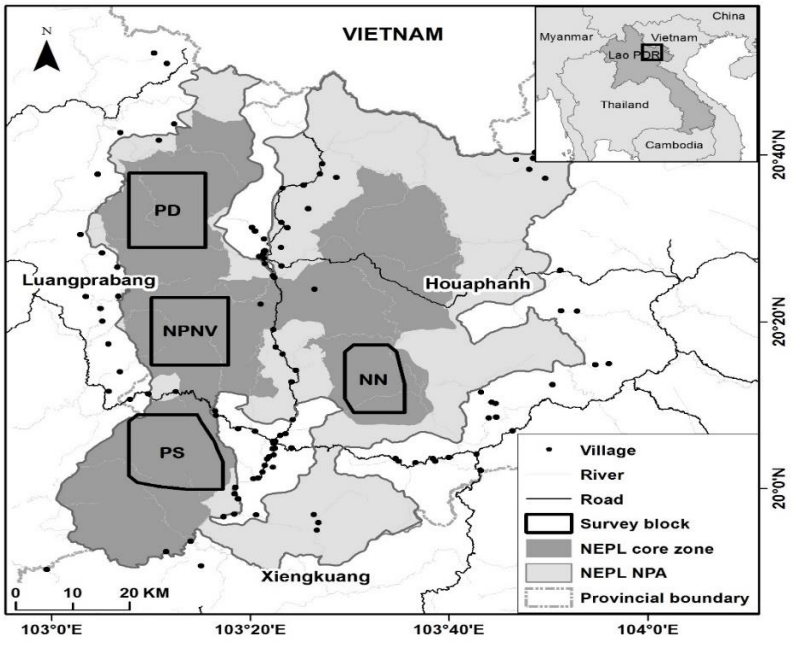


Fig. 1.—The Nam Et - Phou Louey National Protected Area (NEPL), Laos, showing locations of the four survey blocks during 2013 to 2017 (NPNV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou); and NN = Nam Neun). The inset map shows the location of the NEPL in Laos.

For each of the blocks, camera traps were set in pairs at 80 locations (a total of 160 cameras) in a regular grid with 1 – 1.5km spacing and each survey lasted for 49-54 days (Table 1). We used a mixture of infrared camera trap models: CuddeBack Ambush IR (infrared) – Model 1187 camera traps by CuddeBack Digital, Reconyx HYPERFIRE HC500, and MAGINON – WK 3 HD by Supra Foto-Elektronik-Vertriebs-GmbH.

Elevation of trap sites ranged from 629 – 2185m altitude (Table 1); 16% of the sites were below 1000m, 16% were between 1000 to 1500m, and 68% were above 1500m. About 63% of the sites were in closed evergreen and high density semi-evergreen forests while the rest were in shrub/bamboo forest, grassland and regeneration/agricultural areas. The camera traps were placed mostly along ridge lines and animal trails, and at points where trails meet streams. Each camera was mounted onto a tree trunk and its motion sensor was set at 35cm above ground (approx. shoulder height of medium size felid, especially clouded leopards).

Table 1.—Camera trap survey dates, effort and altitude in four blocks in Nam Et - Phou Louey National Protected Area, Laos, during 2013/14, 2015/16 and 2016/17.

Block, site name	Date	Duration (in days)	Stations (cameras)	Trap nights	Altitude (m)
1, Nam Poung - Na Vaen					
	2013	53	80 (160)	3831	983 - 2185
	2015	52	80 (158)	3200	983 - 2185
	2017	52	80 (156)	3530	983 - 2185
2, Pha Daeng					
	2013/2014	51	80 (159)	3693	709 - 1739
	2015	51	80 (156)	3282	709 - 1739
	2017	50	80 (160)	3240	709 - 1739
3, Phoupha - Siphou					
	2014	54	80 (160)	3446	629 - 1514
	2016	50	80 (160)	3003	629 - 1514
	2017	49	80 (160)	1977	629 - 1514

Analyses.—We used spatial capture-recapture (SCR) models to estimate population density of the three felid species from photographical data recorded through our camera trap surveys in 2013, 2016 and 2017.

We identified individuals of the clouded leopard, marbled cat and leopard cat by comparing and matching their pelage patterns from all the camera trap photographs. Records with both right and left flank photographs were matched first and verified based on the location, date and time of encounters before assigning their final identities. In a second step we matched all encounters where we only had either the left or the right flanks. To estimate density, the encounters of all individuals with full identities along with encounters of the flank that had the largest number of captures (either only lefts or only rights) were used. Images of a fourth felid species, the Asiatic golden cat (*Catopuma temminckii*) were captured, but were not individually recognizable and therefore not include in the analysis.

Population density and trends of the clouded leopard, leopard cat and marbled cat were estimated using a SCR model in a Bayesian framework adapted from Royle and Gardner (2011). We extended the basic SCR model to analyse data from three years (sessions) by stacking three independent models that can share parameters. This allowed us to hold λ_0 (the probability of capture when the distance between the animal's activity centre and the trap is zero) and σ (the movement parameters determining the rate of decline in detection probability as function of distance from activity centre to the trap) constant for each species across the three years while allowing for a difference in density. Sharing parameters across session should lead to improved parameters estimates (Sollmann *et al.* 2014a) and given our standardized design we can reasonably assume that detection parameters are comparable across years. While open-population SCR models exist that can directly model survival and recruitment (Gardner *et al.* 2010a), we had too few re-captures of individuals across years to use these models.

We implemented the models in a Bayesian framework and run them in JAGS (Plummer 2003) via R (R Core Team 2017). We used a half-normal detection function and a Poisson encounter

model. The Markov Chain Monte Carlo (MCMC) algorithm was run with 3 MCMC chains with 100,000 iterations and a thinning rate of 10 after discarding the first 50,000 samples.

After estimating a density for each year, we then calculated the trend by taking the ratio between the first and the last survey period (D_1: 2013/14, D_2: 2016/17).

$$Trend = \frac{D_2}{D_1} - 1$$

An important advantage of implementing the model in a Bayesian framework is the facility to obtain a posterior distribution on the change in density, enabling us to derive a point estimate of trend as well as drawing probabilistic conclusions of the genre "We are 90% certain that the population has increased/decreased by 30%".

Results

The cumulative survey effort over all three years was 29,244 trap nights. The percentage of camera theft was 9%, 25% and 34% during the consecutive survey seasons, respectively. The first survey season yielded photographs of 18 clouded leopards, 17 leopard cats, and 19 marbled cats (Table 2). The following two survey seasons yielded photographs of 19 and 10 clouded leopards, 18 and 9 leopard cats, and 15 and 11 marbled cats, respectively (Table 2). Of the clouded leopard individuals, 11 could not be sexed; of those that could be sexed 53% were males. There were 14 and 20 individuals that could not be sexed, for leopard cats and marbled cats, respectively, with 67% and 14% of those that could be sexed were males, respectively. Clouded leopards were detected at 34, 47, and 15 locations; leopard cats at 21, 66, and 13 locations; and marbled cats at 31, 26, and 11 locations in 2013/14, 2015/16 and 2016/17 surveys, respectively.

Table 2.—Records of three felids from 2013/2014, 2015/2016 and 2016/2017 surveys in the Nam Et - Phou Louey National Protected Area, Lao PDR.

	Survey Date	Camera stations	Trap nights	No. photos*	No. individuals (M/F/Unknown)	No. recapt.	Cumulative no. animals detected
Clouded leopard	2013/14	240	10,970	57	18 (7/7/4)	-	18
	2015/16	240	9,485	61	19 (9/7/3)	4	33
	2016/17	240	8,789	24	10 (3/3/4)	2	41
Leopard cat	2013/14	240	10,970	41	17 (4/5/8)	-	17
	2015/16	240	9,485	111	18 (11/2/5)	1	35
	2016/17	240	8,789	48	9 (5/3/1)	5	39
Marbled cat	2013/14	240	10,970	48	19 (1/5/13)	-	19
	2015/16	240	9,485	43	15 (1/8/6)	1	33
	2016/17	240	8,789	32	11 (1/6/4)	2	42

*number of independent photographs or events. No. recapt. = number of recaptured animals

In our density analysis, we assessed model convergence based on Gelman-Rubin diagnostics and the *Rhat* values from MCMC results (at convergence, *Rhat = 1*) and found that all SCR models for the three species had successfully converged. For the clouded leopard, the posterior mean densities for the first and second years were similar, whereas density appeared to decrease the third year (Table 3). The averaged density estimate over all years was 1.70 ± 0.30 individuals/100 km^2. Similarly, for the leopard cat, the estimated mean densities were relatively similar for the first two years, whereas they appeared to decline the third year (Table 3). The estimated mean density of all years was 1.50 ± 0.30 individuals/100 km^2. For the marbled cat, its estimated density declined steadily during all three years (Table 3), and its estimated mean density was 3.80 ± 0.70 per 100 km^2.

The estimates of movement parameters were similar for the clouded leopard and leopard cat, which both were more than twice as high as for the marbled cat (Table 3). The baseline encounter rates were similar for all three species (Table 3).

Based on the posterior distribution of the change in density, there was a 90% probability of a decline in density for the clouded leopard, 93% for the leopard cat, and 83% for the marbled cat. Analysis indicated that we were 83% certain that the clouded leopard population decreased at least 10% during the study. Similarly, we were 88% certain that the leopard cat population declined at least 10%, whereas we were 75% certain that the marbled cat population declined at least 10%.

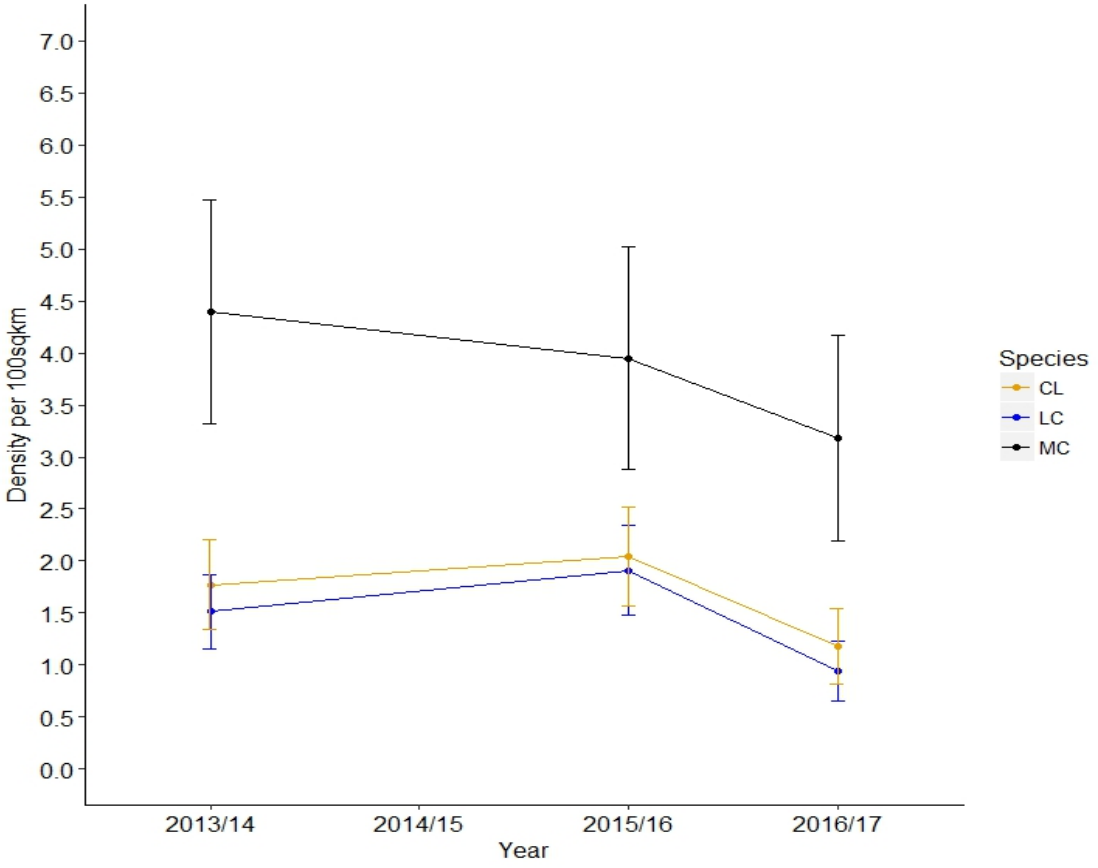


Fig. 2.—Population density (per 100 km^2) and trends since 2013/14 to 2016/17 for the clouded leopard *Neofelis nebulosi* (CL), leopard cat *Priornailurus bengalensis* (LC) and marbled cat *Pardofelis marmorata* (MC).

Table 3.—Summary statistics of spatial capture–recapture models fit to camera-trap data from 2013/14, 2015/16 and 2016/17 on three felid species of the Nam Et - Phou Louey National Protected Area, Lao PDR.

	Clouded leopard		Leopard cat		Marbled cat	
	Mean ± *SD*	95% HPDI	Mean ± *SD*	95% CI	Mean ± *SD*	95% CI
D1	1.77 ± 0.43	1.35 - 2.20	1.51 ± 0.35	1.16 - 1.87	4.40 ± 1.07	3.32 - 5.47
D2	2.04 ± 0.48	1.56 - 2.52	1.91 ± 0.43	1.48 - 2.34	3.95 ± 1.07	2.88 - 5.02
D3	1.18 ± 0.36	0.82 - 1.54	0.94 ± 0.29	0.65 - 1.23	3.18 ± 0.99	2.20 - 4.17
D	1.70 ± 0.30	1.40 - 2.00	1.50 ± 0.30	1.20 - 1.80	3.80 ± 0.70	3.10 - 4.50
σ	3.29 ± 0.37	2.92 - 3.66	3.27 ± 0.37	2.90 - 3.64	1.49 ± 0.18	1.31 - 1.67
λ0	0.03 ± 0.01	0.02 - 0.04	0.04 ± 0.01	0.03 - 0.05	0.05 ± 0.01	0.04 - 0.06

CI, credible interval. D1; D2; D3 & D density are density (per 100km2) for year 2013, 2015, 2017, and average density, respectively. λ0, baseline trap encounter rate (photographs per 10 days). σ, movement parameter (km). N1, 2 & 3 are estimated number of species (for 2013, 2015 and 2017, respectively) within the sampling blocks.

Table 4.—Comparing population density estimates between this study and previously published estimates of the clouded leopard *Neofelis nebulosa*, leopard cat *Priornailurus bengalensis* and marbled cat *Pardofelis marmorata* based on the use of SECR techniques (sorted from smallest to largest estimates)

Site	Density Ind./100 km^2	95% CI	SCR Method	Tiger/Leopard Presence	Source
Clouded Leopard *Neofelis nebulosa*					
Bhutan	0.40 ± 0.1	0.16 - 0.75	Bayesian	Yes	Penjor *et al.* (2018)
Htamanthi Wildlife Sanctuary (Catchment 1), Myanmar	0.60 ± 0.24	0.32 - 1.09	Bayesian	Yes	Naing *et al.* (2017)
NEPL, Laos	1.70 ± 0.30	1.10 - 2.30	Bayesian	Yes/No	This study
Belum, Malaysia	1.83 ± 0.61	0.97 - 3.48	MLH	Yes	Mohamad *et al.* (2015)
Htamanthi Wildlife Sanctuary (Catchment 2), Myanmar	3.05 ± 1.03	1.27 - 5.06	Bayesian	Yes	Naing *et al.* (2017)
Temengor, Malaysia	3.46 ± 1.00	1.98 - 6.04	MLH	Yes	Mohamad *et al.* (2015)
Manas National Park, India	4.73 ± 1.43	*	MLH	Yes	Borah *et al.* (2013)
Dampa Wildlife Reserve, India	5.14 ± 1.80	2.05 - 8.72	Bayesian	No	Singh and Macdonald (2017)
Leopard cat *Priornailurus bengalensis*					
NEPL, Laos	1.5 ± 0.30	1.00 - 2.00	Bayesian	Yes/no	This study
Bilingiri Rangaswamy Temple Tiger Reserve, India	4.48 ± 1.31	2.17 - 7.08	Bayesian	Yes	Srivathsa *et al.* (2015)
Deramakot Forest Reserve, Sabah Malaysia	9.60 ± 1.70	6.69 - 12.98	Bayesian	No	Mohamed *et al.* (2013b)

Bhadra Tiger Reserve, India	10.45 ± 3.03	5.14 - 16.50	Bayesian	Yes	Srivathsa *et al.* (2015)
Tang Kulap-Pinangah Forest Reserve, Sabah, Malaysia	12.40 ± 1.6	9.49 - 15.73	Bayesian	No	Mohamed *et al.* (2013b)
Segaliud Lokan Forest Reserve, Sabah, Malaysia	16.5 ± 2.00	12.99 - 16.37	Bayesian	No	Mohamed *et al.* (2013b)
Khangchendzonga Biosphere Reserve, India	17.52 ± 5.52	8.80 - 26.80	Bayesian	No	Bashir *et al.* (2013)
Marbled cat *Pardofelis marmorata*					
NEPL, Laos	3.80 ± 0.70	2.60 - 5.50	Bayesian	Yes/no	This study
Dampa Wildlife Reserve, India	5.03 ± 2.07	1.67 - 9.50	Bayesian	No	Singh and Macdonald (2017)
Tawau, Sabah, Malaysia	7.10 ± 1.90	3.81 - 10.73	Bayesian	No	Hearn *et al.* (2016b)
Htamanthi Wildlife Sanctuary, Myanmar	8.80 ± 2.00	*	Bayesian	Yes	Naing *et al.* (2017)
Tabin Nortu Sabah, Malaysia	10.45 ± 3.38	4.28 - 16.91	Bayesian	No	Hearn *et al.* (2016b)
Danum valley Sabah, Malaysia	19.57 ± 8.36	6.87 - 36.65	Bayesian	No	Hearn *et al.* (2016b)

CI: confidence interval for Maximum likelihood or credible interval for Bayesian; Ind: Individual; MLH: Maximum Likelihood Method; SCR: Spatially Explicit Capture-Recapture; *: not available.

Discussion

We present the first systematic study of clouded leopard, leopard cat and marbled cat in Lao PDR. Alarmingly, across just three years in one of the most important protected areas in Southeast Asia, we found significant declines in density for clouded leopard and leopard cat, with evidence, albeit not significant, of a decline for marbled cat too. These declines were against a background of evidence that snaring began and exponentially increased in NEPL from 2008 to 2012 (Johnson *et al.* 2016). Snaring has not been quantified in NEPL since 2013, but we assume it has continued to increase in NEPL until the present, especially given a similar trend can be seen throughout Southeast Asia (Gray *et al.* 2017a; Gray *et al.* 2017b). Therefore, we infer that increases in snaring caused the decline of all three felid species during our study. We detected no evidence of mesopredator release following the extirpation of tiger and leopard, but any such effect could easily have been masked by the impact of snaring. Compared to previous studies, our density estimate for clouded leopard was within the range reported for this species (Table 4). Interestingly, the highest density of clouded leopard was reported from the only site where tiger and leopard were absent (Table 4). Our density estimates for both leopard cat and marbled cat were the lowest ever reported for these species (Table 4). The pattern across studies appeared to show that the highest reported densities of leopard cat and marbled cat were from sites where tiger and leopard were absent (Table 4) which is unexpected under the mesopredator release hypothesis.

While habitat loss is ultimately a significant threat to clouded leopard (Cushman *et al.* 2017), our wider habitat modelling indicates that NPA is still suitable for them Macdonald *et al.* (submitted). We therefore deduce that the observed decline is a result of intensive snaring prompted by the illegal wildlife trade. There is evidence of increased targeting of clouded leopard for traditional medicine markets, skins and bones for decoration, and live animals as pets since 2005 (D'Cruze and Macdonald 2015). Although our density estimates suggest that

clouded leopard is still viable in NEPL, there are no grounds for complacency, as the density trend expectedly would continue unless snaring is brought under control.

The posterior means of the densities of leopard cat over three years were very similar to the estimates of the clouded leopard. The minimal difference between the first two years were followed by a two-fold drop in the third year. The leopard cat, while relatively common throughout its range (Ross *et al.* 2015), is primarily ground dwelling (Mohamed *et al.* 2013b) and therefore is vulnerable to snaring (Johnson *et al.* 2016). Our density estimate for the leopard cat was the lowest recorded for this species, which raises further concern about the impact of snaring. Similar to the clouded leopard, the leopard cat density expectedly would continue to decline unless snaring is reduced.

The marbled cat showed a declining trend in density across three years, although it was not statistically significant. This trend is expected under the mesopredator release hypothesis. However, globally, the population of this species is also declining, due to habitat loss and hunting via targeted and indiscriminate snaring (Ross *et al.* 2016). Similar to the leopard cat, our density estimate for the marbled cat was the lowest reported anywhere in Southeast Asia (Table 4), suggesting that snaring also is likely causing the low density of this species in NEPL. We speculate that the density of marbled cats in NEPL may nonetheless also be the highest estimate in Laos insofar as records for the species elsewhere in the country are few (Coudrat *et al.* 2014).

Overall, the declining trend for all species is consistent with the high turn-over in individuals from one year to the other (Table 2) and the increasing theft of cameras across years (from 9% to 34%). Although snaring has not been quantified since 2013, the firmly rooted opinion amongst protected area staff and our field teams in NEPL is that it has continued to proliferate since the exponential increase recorded from 2008 to 2012 (Johnson *et al.* 2016). Meanwhile snaring has been judged to have caused of the extirpation of tiger and leopard in NEPL (Johnson *et al.* 2016; Ripple *et al.* 2016; Gray *et al.* 2017a; Gray *et al.* 2017b).

What action should follow our findings? Obviously, intensified removal of snares, better patrolling and enforcement of regulations, and education and involvement of local people. These suggestions are easily made, but extremely difficult to implement, and so we emphasise the immediate and considerable threat to these felids. In other areas of Southeast Asia, poaching within protected areas has been reduced using these methods. For example, in Kuiburi National Park, Thailand, a community outreach program resulted in a decrease in poaching and recovery of hunted wildlife populations within the park (Steinmetz *et al.* 2014). In Huai Kha Khaeng Wildlife Sanctuary, Thailand, the development of systematic and intensified enforcement regime was developed, which included the collection of detailed data by rangers in the field, along with increased patrol days and patrol distances (Duangchantrasiri *et al.* 2016). This effective enforcement regime was successful in reducing poaching and maintaining the tiger density in the sanctuary (Duangchantrasiri *et al.* 2016). Given the success demonstrated by community outreach and intensive and systematic patrol regimes, we recommend that both of these strategies be immediately implemented in NEPL to avert the extirpations of the remaining members of the felid community.

ACKNOWLEDGMENTS

We thank the Wildlife Conservation Society, Lao PDR, for their and the Nam Et-Phou Louey National Protected Area for their extensive in-kind support and for their efforts towards planning and implementing the research. For data collection and management, we thank Mr. Phonesouk Chanthalavong for his excellent assistance in field work preparation and implementation, and data management. We further thank Mike Meredith, and Ngumbang Juat for their guidance. The research was supported by a grant to DWM from the Robertson Foundation and National Geographic Society, for which we are deeply grateful.

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Supplementary Data SD1 .—Example JAGS code for three sessions density estimation

```
# Three Sessions density estimation with JAGS for Clouded Leopards (CL) in NEPL
# The data combined into one survey sessions of 50 days period
#The data are from 3 survey blocks over 3 years 2013 - 2017
#This model is based on the assumption that sigma and g0 don't change while density varies across the three seasons
# ==============================

# Load the 'secr' package
library(jagsUI)
library(wiqid)                  # for plotting functions
library(secr)

#############################################################
#### Define state space or study area ###################
#############################################################

# Trap locations for all seasons:
#Co-ordinates are in km.
all.traps <- read.traps("TDF_all seasons.txt") #TDF is trap data file

# If not using the mask in the analysis, define the extent this way
(xl <- min(all.traps$x) - 15)     # 15km (should be adjusted based on the species of interest
(xu <- max(all.traps$x) + 15)
(yl <- min(all.traps$y) - 15)
(yu <- max(all.traps$y) + 15)

# Area:
( A <- (xu - xl) * (yu - yl) )     #  4649.671 km2 with buffer = 15km

#########################
#### Read in the data and create capture history for each survey session
#### Produce 3D arrays consisting of: Individuals, occassions, and trap locations
```

```
##########################

## For Season One - 2013
cl.ch1 <- read.capthist("CL_EDF_sess1.txt", "TDF_sess1_km.txt", detector = "proximity", fmt= "trapID", noccasions = 55)


## For Season Two - 2015
cl.ch2 <- read.capthist("CL_EDF_sess2.txt", "TDF_sess2_km.txt", detector = "proximity", fmt= "trapID", noccasions = 53)

## For Season Three - 2017
cl.ch3 <- read.capthist("CL_EDF_sess3.txt", "TDF_sess3_km.txt", detector = "proximity", fmt= "trapID", noccasions = 53)

#############################################################################
# Convert to a y[animal, trap] matrix with number of captures:
###################
## Season One
yObs1 <- apply(cl.ch1, c(1, 3), sum)  # "1" is the animal ID information and "3" is the detector IDs
head(yObs1)
dim(yObs1)  # checking 18 individuals, 240 traps

# data = maximum number of captures per trap per animal, summed over all occasions.
max(yObs1)

# number of locations where each individual was captured
(cl.obs1 <- rowSums(yObs1))

J1 <- ncol(yObs1)       # number of trap deploy in season 1

## Season two
yObs2 <- apply(cl.ch2, c(1,3), sum)
head(yObs2)
```

```
dim(yObs2)
max(yObs2)
(cl.obs2 <- rowSums(yObs2))
J2 <- ncol(yObs2)       # number of trap deploy in season 2

## Season three
yObs3 <- apply(cl.ch3, c(1,3), sum)
head(yObs3)
dim(yObs3)
max(yObs3)
(cl.obs3 <- rowSums(yObs3))
J3 <- ncol(yObs3)       # number of trap deploy in season 3

#######################################
# Extract the traps information
#################################################
traps1 <- as.matrix(traps(cl.ch1))       #traps information for season 1
traps2 <- as.matrix(traps(cl.ch2))       # traps information for season 2
traps3 <- as.matrix(traps(cl.ch3))       # traps information for season 3

#########################################################
###### JAGS model ######################################

cat("model{
# Priors distributions for the session-invariant parameters
sigma~dunif(0, 15)   #adjust to your species
sigma2<-2*sigma*sigma

#Expected encounter rate at distance zero to Activity Centre
lam0 ~ dgamma(0.1,0.1)

        # session 1
        psi1 ~ dunif(0, 1)  # Data augmentation parameter

        # Likelihood
```

```
        for (i in 1:M){            # loop through the population for session 1
         z1[i] ~ dbern(psi1)
         SX1[i] ~ dunif(xl,xu)          # priors for the activity centers
         SY1[i] ~ dunif(yl,yu)          # for each individual i
  for(j in 1:J1) {         #loop through the J1 trap locations
dist21[i,j] <- pow(SX1[i]-trapmat1[j,1], 2) + pow(SY1[i]-trapmat1[j,2],2)  # Distance^2
                  # A decreasing function between AC of i to trap j
g1[i,j] <- exp(-dist21[i,j]/sigma2)
# Detection probability, K is number of survey occasions
pmean1[i,j] <- K1[j] * g1[i,j] * lam0 * z1[i]
                  y1[i,j] ~ dpois(pmean1[i,j])    # Encounter frequency
                                 }
                           }

        N1 <- sum(z1[1:M])                                                    #derive
number (check against M)
        D1 <- N1 / A                                                          #derive
density over state space


        # session 2
        psi2 ~ dunif(0, 1)
        #Likelihood
        for (i in 1:M){            # loop through the population for session 2
         z2[i] ~ dbern(psi2)
         SX2[i] ~ dunif(xl,xu)          # priors for the activity centers
         SY2[i] ~ dunif(yl,yu)          # for each individual

           for(j in 1:J2) {  #loop through the J2 trap locations
dist22[i,j] <- pow(SX2[i]-trapmat2[j,1], 2) + pow(SY2[i]-trapmat2[j,2],2)  # Distance^2

# A decreasing function between AC of i to trap j
g2[i,j] <- exp(-dist22[i,j]/sigma2)

# Detection probability, K is number of survey occasions
```

```
pmean2[i,j] <- K2[j] * g2[i,j] * lam0 * z2[i]
                    y2[i,j] ~ dpois(pmean2[i,j])    # Encounter frequency
                                }
                            }
N2 <- sum(z2[1:M])
D2 <- N2 / A

# session 3
        psi3 ~ dunif(0, 1)
        #Likelihood
        for (i in 1:M){
                z3[i] ~ dbern(psi3)
                SX3[i] ~ dunif(xl,xu)
                SY3[i] ~ dunif(yl,yu)

                for(j in 1:J3) {
dist23[i,j] <- pow(SX3[i]-trapmat3[j,1], 2) + pow(SY3[i]-trapmat3[j,2],2)  # Distance^2
                g3[i,j] <- exp(-dist23[i,j]/sigma2)
                pmean3[i,j] <- K3[j] * g3[i,j] * lam0 * z3[i]
                y3[i,j] ~ dpois(pmean3[i,j])
                        }
                        }
        N3 <- sum(z3[1:M])
        D3 <- N3 / A

trend <- D3 / D1 - 1
D <- (D1 + D2 + D3) / 3         #Average density from three season

}
  ", file = "CL_3sess_SCR.txt")
```

```
#################################################################

#Prepare data for JAGS
```

```
# ----------------------------
# Create the augmented captures matrix:
M <- 180 # Number of capture histories after augmentation
# Number of survey occasions, This can be different for different seasons
K1 <- read.table("K1.txt")[,1]
K2 <- read.table("K2.txt")[,1]
K3 <- read.table("K3.txt")[,1]

# Capture matrix y is an M x traps matrix with number of captures:
#180 by 240 locations
y1 <- rbind(yObs1, matrix(0, M - nrow(yObs1), J1))
y2 <- rbind(yObs2, matrix(0, M - nrow(yObs2), J2))
y3 <- rbind(yObs3, matrix(0, M - nrow(yObs3), J3))
dim(y1)
dim(y2)
dim(y3)

# Specify the data in a list, for shipment to JAGS:
jagsdata = list(y1 = y1, y2 = y2, y3 = y3, M = M, xl = xl, xu = xu, yl = yl, yu = yu, A = A, J1 =
J1, J2 = J2, J3 = J3, trapmat1 =traps1, trapmat2 =traps2, trapmat3 =traps3, K1 =
as.vector(K1), K2 = as.vector(K2), K3 = as.vector(K3))

str(jagsdata)

# Initial values for z:
inits <- function() list(z1=rep(1,M), z2=rep(1,M), z3=rep(1,M))

wanted <- c("trend", "N1", "N2", "N3", "D1", "D2", "D3", "psi1", "psi2", "psi3", "lam0",
"sigma", "D")



#####################################################
# Run the model
cljags <- jags(jagsdata, inits=inits, wanted, model.file="CL_3sess_SCR.txt", n.chains=3,
n.iter=100000, n.burnin=50000, n.thin=10, parallel=TRUE, DIC=FALSE)
```

```
#save the results
save(cljags, file="cljags_3sess_100k.Rdata")

# Check the results
load("cljags_3sess_100k.Rdata") #load the saved results
cljags
plot(cljags)
View(cljags)
```

Chapter 4

Spatial co-occurrence and activity patterns of sympatric felids and dhole in Nam Et - Phou Louey National Protected Area, Lao PDR.

Submitted to *Journal of Animal Ecology*

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Summary

Niche differentiation of coexisting species that are ecologically similar may occur in one or more niche dimensions. Nam Et - Phou Louey National Protected Area (NEPL) is known for its diversity in carnivore communities yet little is known regarding their ecology.

This study aimed to investigate how five carnivore species (dhole *Cuon alpinus*, clouded leopard *Neofelis nebulosa*, Asian golden cat *Catopuma temminckii*, leopard cat *Prionailurus bengalensis*, and marbled cat *Padofelis marmorata*) coexist in the NEPL in order to insinuate the degree of their interactions. We used camera trap data from 2013 – 2017 for this study.

The multispecies occupancy modelling in Bayesian framework was adopted to measure co-occurrence patterns between species and determine habitat factors influencing their occurrence. The circular statistics and kernel density approaches were used to determine the diel activity patterns of each species and quantify the temporal overlap between species in the selected pairs. We found no influence of dhole presence on clouded leopard and Asian golden cat occupancy. There was a slight positive association between clouded leopard presence and the Asian golden cat occupancy while the leopard cat was most likely to use the same sites as the Asian golden cat. Similarly, there was a slight evidence to show that marbled cat likely shared the same sites as the Asian golden cat and the leopard cat. Dhole occurrence were positively associated with density of settlement areas while avoiding mosaic areas. While there was no evidence that any of the habitat covariates influenced clouded leopard, leopard cat and marbled cat occupancy, the Asian golden cat was positively associated with areas of high tree cover and grasslands. We found that the dhole was strongly diurnal, although somewhat active around dusk. The clouded leopard was predominantly crepuscular and most active at dawn. The Asian golden cat was active both by day and by night, and with a peak in activity at dawn. The leopard cat was strongly nocturnal whereas the marbled cat was strongly diurnal, although crepuscular. The coincidence in activity was greatest between the clouded leopard and the Asian golden cat, while the greatest difference was between the leopard cat and the marbled cat. The Asian golden

cat exhibited a tendency to cathemerality, and we speculate that dietary specialisation, rather than temporal segregation, facilitates its coexistence with competitors. Similarly, we deduce dietary specialisations distinguish the leopard cat and marbled cat, themselves clearly temporally segregated, from the Asian golden cat with whose activity patterns they overlap. Our study documents spatial and temporal aspects of niche characteristics for little known top predators of S.E. Asian forests, and in particular the unusually rich community of medium and small carnivores in NEPL.

Key words: activity overlap; camera traps; dhole; felids; Laos; Nam Et-Phou Louey; species interaction.

Introduction

Species coexistence is one of the most studied and complex field in ecology (Gordon 2000). In principle, species that are ecologically similar cannot coexist in the same area (Gause 1934; Hardin 1960). For such species to coexist there should be some degree of niche differentiation whereby negative interspecific competition is minimised (Schoener 1974). Niche differentiation of coexisting species that are ecologically similar may occur in one or more niche dimensions which include space, time and food (Case and Gilpin 1974; Schoener 1974). Information on species' niche differentiation not only helps us to understand the capacity of species to coexist but it also enhances biodiversity conservation especially within communities where top predators have been extirpated (Estes *et al.* 2011; Ripple *et al.* 2014).

Nam Et - Phou Louey National Protected Area (hereafter NEPL) is known for its diverse carnivore community (Johnson *et al*. 2009), yet little is known regarding the ecology of those carnivore species. Large predators, tiger *Panthera tigris* and leopard *P. pardus*, were once part

of the communities. Currently, the canid and felid communities of the NEPL consist of medium-sized (i.e., dhole *Cuon alpinus,* clouded leopard *Neofelis nebulosa*, and Asian golden cat *Catopuma temminckii*) and small-sized carnivores (i.e., marbled cat *Pardofelis marmorata*, leopard cat *Prionnailurus bengalensis*). To date, few studies have examined their occurrence and activity patterns at the protected area level (Johnson *et al.* 2009; Kamler *et al.* 2012). However, their coexistence has not been explored and very few studies are available from elsewhere within their range looking at factor affecting their distribution and degree of interactions for some of these species (Ngoprasert *et al.* 2012; Hearn *et al.* 2013; Lynam *et al.* 2013; Ross *et al.* 2013; Mohamed *et al.* 2016; Hearn *et al.* 2018b). This study aimed to investigate how canid and felid species coexist in the NEPL in order to insinuate the degree of their interactions.

One of the mechanisms facilitating coexistence of ecologically similar species is their spatial niche partitioning (Wereszczuk and Zalewski 2015). Theoretically, when food sources are limited and the dietary overlap between species (with similar ecological requirements) is high, there is a high likelihood of interference between the competing species where dominant predators can affect the population of subordinate predators (Linnell and Strand 2000). In such circumstances, subordinate competitors may display different ecological niches like preference or utilisation of different habitat types to avoid potentially unpleasant encounters with superior competitors (Witczuk *et al.* 2015). In carnivore communities, while prey density might influence occurrence of top predators, other habitat factors may explain the occurrence of subordinate predators.

The dhole (10 – 20kg), listed as Endangered by the IUCN (Kamler *et al*. 2015), is a hypercarnivore and group living species with often > 10 members (Johnsingh 1985; Van Valkenburgh 1991; Kamler *et al.* 2015). The species is habitat generalist using various habitats from dense evergreen forest to open dry dipterocarp forest (Duckworth *et al.* 1999b). Dhole prefers to prey upon medium sized ungulates (40 – 60kg; Selvan *et al.* 2013a) but where prey

species of such size are available at very low density, they were reported to selectively prey upon both small (20 – 28kg) and large (>100kg) ungulate species (Kamler *et al.* 2012). The clouded leopard (11- 23kg), listed as Vulnerable by the IUCN (Grassman *et al*. 2016), is highly arboreal species (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Grassman *et al.* 2005a; Austin *et al.* 2007). The species is known to be strongly associated with forest habitat, especially primary evergreen forest (Grassman *et al.* 2005a; Austin *et al.* 2007) but there were some records from dry deciduous, secondary, and logged forests, shrub and grasslands (Nowell and Jackson 1996; Grassman *et al.* 2015). There is a degree of overlap with dhole in terms of the clouded leopard's prey, which includes small and medium sized ungulates as well as primates, porcupines, squirrels, and pheasants (Grassman *et al*. 2005a). The Asian golden cat (9 – 16kg), listed as Near Threatened by the IUCN (McCarthy *et al*. 2015), also is often associated with closed forest habitats (Nowell and Jackson 1996; Grassman *et al.* 2005a; McCarthy *et al.* 2015a; McCarthy *et al.* 2015b). Asian golden cat was also recorded in grasslands and fragmented forests (Duckworth *et al.* 1999b). Its diet is more similar to that of the clouded leopard than that of the dhole, and includes muntjacs, squirrels and small rodents (Grassman *et al.* 2005a). The leopard cat (3 – 7kg), listed as Least Concern by the IUCN (Ross et al. 2015), is more of a habitat generalist and its diet overlaps partially with that of the Asian golden cat and the marbled cat, although it feeds primarily on small rodents (Ghimirey and Ghimire 2010; Macdonald *et al.* 2010a; Lorica and Heaney 2013; Mohamed *et al.* 2013b; Ross *et al.* 2013; Ross *et al.* 2015). The marbled cat (2 – 5kg), listed as Near Threatened by the IUCN (Ross *et al.* 2016), is primarily associated with wet evergreen and semi-evergreen forests (Nowell and Jackson 1996; Duckworth *et al.* 1999b; Grassman *et al.* 2005a) although there are some records from disturbed and logged forests (Mohamed *et al.* 2009; Mathai *et al.* 2010; Ross *et al.* 2010). Although there are no detailed dietary studies of marbled cat, it is assumed that they feed primarily on birds and small rodents, including squirrels (Ross *et al*. 2016), and

therefore have some dietary overlap with leopard cat. With these characteristics of these five species in mind, their interactions could further be explored.

Spatial dimensions are thought to be important more often than other dimensions in niche differentiation (Schoener 1974), whereas temporal dimension is observed less often (Schoener 1974; Ritchie and Johnson 2009). However, temporal partitioning can happen when level of similarity in spatial niche and food resources is high (Valeix *et al.* 2007; Harrington *et al.* 2009; Valeix *et al.* 2009) whereby subordinate predator may adjust their activity patterns upon presence of dominant species in order to stabilize coexistence. With that being said, dhole was reported to be exclusively diurnal (Kamler *et al.* 2012), whereas clouded leopard is known to be primarily nocturnal with crepuscular activity peaks (Grassman *et al.* 2005a; Austin *et al.* 2007). Previous study suggested that Asian golden cat is mainly diurnal with also crepuscular activity peaks (Grassman *et al.* 2005a) whereas marbled cat is primarily diurnal (Singh and Macdonald 2017). The leopard cat on the other hand are reported to be predominantly nocturnal while also found to exhibit crepuscular pattern in some areas (Grassman *et al.* 2005c; Macdonald *et al.* 2010a; Lynam *et al.* 2013; McCarthy *et al.* 2015b) which could be affected by presence of other carnivores.

To further investigate coexistence to infer interactions among these five species, the objectives of this study therefore were to: (i) measure co-occurrence patterns between species; (ii) determine habitat factors influencing their occurrence; (iii) determine the diel activity patterns of each species; and (iv) quantify the temporal overlap between the species. Based on the habitat, ecology and relative body size, of these species, we make the following predictions:

P1. There is a positive spatial association and low temporal overlap between the dhole and the clouded leopard.

P2. Occupancy of the Asian golden cat is negatively affected by occupancy of dhole while their temporal overlap is high.

P3. Occupancy of the clouded leopard negatively affect occupancy of the Asian golden cat with low temporal overlap between them.

P4. The Asian golden cat occupancy negatively affects occupancy of marbled cat but not that of the leopard cat, and the temporal overlap between the Asian golden cat and the marbled cat is higher than the overlap between the Asian golden cat and the leopard cat.

P5. There is a positive association between leopard cat and marbled cat occurrence with low temporal overlap between them.

We test these predictions using camera trap data from NEPL collected during 2013 to 2017 survey.

Materials and Methods

Study area – The NEPL NPA is in the northern highlands of Lao PDR (between latitude 19°50' - 20°50'N and longitude 103°00' - 103°53'E), bordering Vietnam along its northern boundary (Fig.1). It covers an area of 5,969 km^2 with rugged topography across seven districts and three provinces (Houaphan, Luang Prabang, and Xiengkhuang) and elevation ranging from 400 - 2257 m, of which >60% is above 1000 m and 91% with slopes >12% (Johnson 2012). Vegetation is largely dominated by dry evergreen and semi-evergreen forests. However, around one third of the park is degraded forest with a canopy cover of less than 20%. The climate in Laos is tropical monsoonal with a rainy season lasting from May to October followed by a distinct dry season for the remainder of the year. Annual rainfall ranges from 1400 to 1800 mm (Duckworth *et al.* 1999b; Johnson 2012). The NEPL is divided into two protected zones; a totally protected core zone where human activity is prohibited and a managed use zone (Fig.1).

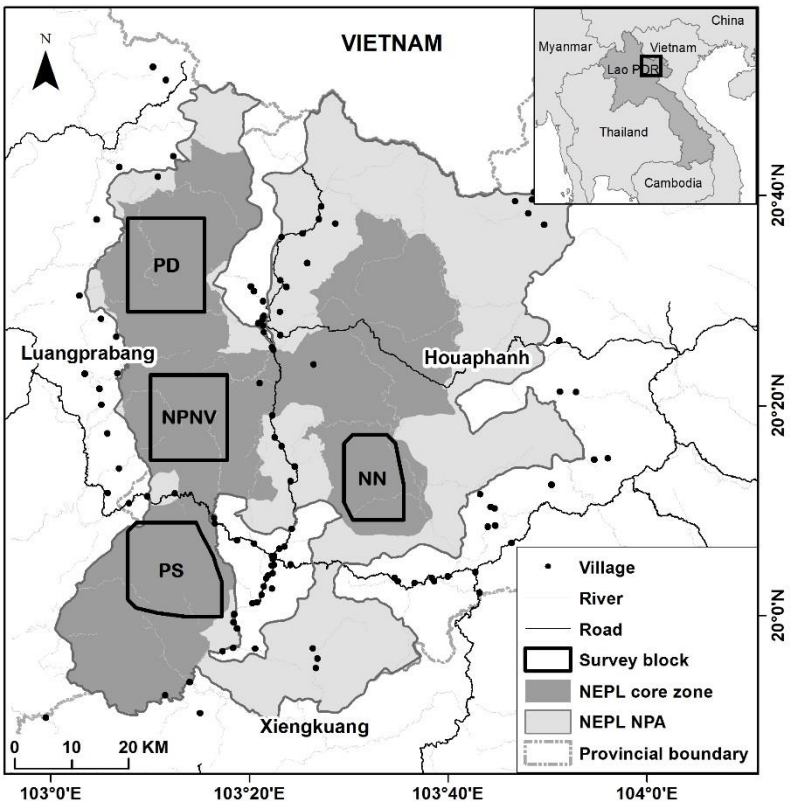


Fig.1: The Nam Et - Phou Louey National Protected Area (NEPL), Laos, showing locations of the four survey blocks during 2013 to 2017 (NPNV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; NN = Nam Neun). The inset map shows the location of the NEPL in Laos.

Camera trapping – Systematic camera trap surveys were carried out from 2013 to 2017 within the NEPL core zone, in four ~200 km^2 blocks (Fig.1). These four sampling blocks are known as Nam Poung - Na Vaen (NPNV); Pha Daeng (PD); Phoupha - Siphou (PS); and Nam Neun (NN). For each of the blocks, camera traps were set in pairs at 80 locations, except for block NN where cameras were set at only 60 locations, and at 1 – 1.5km spacing. We used a mixture of infrared camera trap models: CuddeBack Ambush IR (infrared) – Model 1187 camera traps by CuddeBack Digital, Reconyx Hyperfire HC500, and MAGINON – WK 3 HD by Supra Foto-Elektronik-Vertriebs-GmbH.

Traps sites were from 629 – 2185m altitude (Table 1) where 16% of the sites are at below 1000m, 16% are at between 1000 to 1500m, and 68% are at above 1500m. About 63% of the sites are in closed forest – evergreen and high density semi-evergreen forests. The camera traps were placed mostly along ridge lines and animal trails, and at points where trails meet streams. Each camera was mounted onto a tree trunk and ensured that its motion beam was set at 35cm height from the ground at the centre of the trail (approx. shoulder height of medium size felid, especially clouded leopards). Each survey period lasted for a minimum of 50 days (Table 1).

Table 1: Camera trap survey dates, effort and altitude in four blocks in Nam Et - Phou Louey, Laos, during 2013 – 2017 (NPNV = Nam Poung - Na Vaen; PD = Pha Daeng; PS = Phoupha - Siphou; NN = Nam Neun).

Block name	Survey year	Date	Duration (days)	Sites (cameras)	Trap days	Altitude (m)
NPNV	1	3 – 5/2013	53	80 (160)	3831	983 – 2185
	2	3 – 5/2015	52	80 (158)	3200	
	3	2 – 4/2017	52	80 (156)	3530	
PD	1	11/2013 – 1/2014	51	80 (159)	3693	709 – 1739
	2	5 – 7/2015	51	80 (156)	3282	
	3	4 – 5/2017	50	80 (160)	3240	
PS	1	2 – 4/2014	54	80 (160)	3446	629 – 1514
	2	2 – 4/2016	50	80 (160)	3003	
	3	6 – 8/2017	49	80 (160)	1977	
NN	1	5 – 7/2014	54	60 (120)	2825	720 – 1522

Occupancy. – To test for spatial associations between species and evaluate the effect of site covariates on occupancy, we adopted a Bayesian multi-species occupancy modelling framework following the approach by Waddle *et al.* (2010). With this hierarchical modelling approach, occupancy and detection parameters can be simultaneously estimated for multiple species. With the flexibility of this framework, modelling the influence of one species (dominant) occupancy on occupancy and detection of other species (subordinate) was possible. Like the general occupancy framework, three basic model assumptions are retained (MacKenzie *et al.* 2002). First, occupancy state is "closed" (i.e., species occupancy does not change during the survey period). Second, sites and occasions are spatially and temporally independent. Third, there is no unexplained heterogeneity in occupancy and detection. We relaxed these three assumptions, respectively, by interpreting probability of site occupancy as probability of site use, acknowledging that arbitrary choice of occasion length may result in temporal dependence, and recognising a compromise between model complexity and interpretation when including covariates on occupancy and detection modelling (Cusack *et al.* 2017).

Here we considered the following hierarchical interaction models between the co-occurring species:

a. Dhole presence affects clouded leopard occupancy (ψ) and detection (p). Despite similar body size, we assumed that the dhole is dominant to the clouded leopard based on the fact that dholes are pack living species. Any direct encounter between them was assumed to be between a pack of dholes and a clouded leopard (or a mother and with a couple of cups) in which case dholes have more advantage.
b. Dhole presence affects Asian golden cat ψ and p. In this case we made the same assumption as above along with considering the relative body size.
c. Based on relative body size, Asian golden cat presence affects ψ and p of leopard cat
d. Asian golden cat presence affects marbled cat ψ and p due to the relative body size.

e. Leopard cat presence affects marble cat ψ and p, based on the relative body size.

Based on previous study (Jenks *et al.* 2012; Srivathsa *et al.* 2014; Hearn *et al.* 2016a; Hearn *et al.* 2016b; Hearn *et al.* 2016c; Mohamed *et al.* 2016; Hearn *et al.* 2018a; Hearn *et al.* 2018b; Macdonald *et al.* submitted) covariates that we considered for modelling occupancy include elevation (Jarvis *et al.* 2008), roughness accounting for topographic heterogeneity was derived from the digital elevation layer using the Geomorphometry & Gradient Metrics Toolbox (Evans *et al.* 2014) in ArcGIS 10.2.2 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011), percent forest cover (Hansen *et al.* 2013), settlement/village density (calculated using Kernel Density tool in ArcGIS) and four land cover categories (ESA 2015 was refined with NEPL NPA land cover layer from 2015). The land cover categories consist of agriculture, forest, grassland and mosaic (regenerating). For each land cover category, we calculated the percentage of the landscape occupied by each land cover type (PLAND). We also included prey encounter rate (PER), which was the number of independent events (>1 hour interval) per 100 trap days (Carbone *et al.* 2001). For each carnivore, separate PER was calculated based on their known prey species and was considered for both occupancy and detection modelling. We used camera trap data from 2015/2016 (second survey season) for this part of the analysis because number of independent events for most species in questions and single-season occupancy modelling was implemented.

Prior to performing occupancy modelling in Bayesian framework, collinearity of continuous site covariates was assessed by pairwise correlation using Spearman's rank correlation coefficients (Dormann *et al.* 2013). Any combination of covariates that have a pairwise correlation > 0.7 was considered correlated and the most informative covariates were retained for final modelling process. Selection of the covariates for each species were done via testing for the most informative variables using single-species, single-season habitat use models in the R package "unmarked" version 0.12-2 (Fiske and Chandler 2011) in R 3.4.3 (R Core Team 2017) following a two-step process as described by Long *et al.*(2011). Once habitat covariates

for each species were selected, they were integrated into a Bayesian framework to estimate their effects as well as to control for their effects on our interaction model. Obtaining conditional estimates of occupancy and detectability was not part of this analysis objective.

Detection history for each species was compiled separately where a 0 and a 1 denote non-detection and detection, respectively, in a survey period/site. Data from five trap days at the site were aggregated as a single survey occasion, following Johnson *et al*. (2009). Overall, there were 10 sampling occasions. The occupancy modelling approach that we used accommodates sites with incomplete survey histories or histories with missing values (e.g., a camera was not deployed in one particular occasion).

Given the low number of detections for all of the species, our data were inadequate for precise estimates of some parameters associated with occupancy interaction effects. Our preliminary analyses showed that posterior estimates of occupancy interaction effects of all assumed dominant species were pushed against boundaries of flat priors. Following the similar situation as the study by Bischof *et al.* (2014), we decided to use relatively narrow priors with a normal distribution (mean = 0, precision = 0.1) for all species occupancy interaction effects and compared the extent and direction of the posterior distribution's deviation from 0 to assess the level of support for avoidance or association. We used uninformative priors with a uniform distribution defined on the log-odds [-10, 10] for other parameters. We fitted the Bayesian model in JAGS (Plummer 2003) via R platform (R Core Team 2017). The Markov Chain Monte Carlo (MCMC) algorithm was run for 600,000 iterations, for 3 chains with the thinning rate of 50 and discarding the first 100,000 samples. We assessed convergence using the Gelman-Rubin statistic where value <1.1 denotes convergence (Gelman and Rubin 1992).

Circadian activity and overlap analysis – Species activity patterns were examined using circular statistics (Zar 1996). Percentage of detections recorded for each hour over a 24-hour period was used in the modelling following Ross *et al.* (2013). Diel activity pattern models

were fitted as a function of continuous trigonometric predictors describing one (*cosΘ*, *sinΘ*) and two (*cos2Θ*, *sin2Θ*) complete cycles in a 24-hour period with $\Theta = \pi t/24$, where *t* is time in hours (Ross *et al.* 2013). With *cosΘ*, a species is determined nocturnal with positive coefficient or diurnal with negative coefficient. With *sinΘ*, a species is determined crepuscular with single activity peak either at dawn (if positive coefficient) or dusk (if negative coefficient). With the bimodal (*cos2Θ*), a species is crepuscular and active at both dawn and dusk (if negative coefficient) or at both midday and midnight (if positive coefficient). As for coefficients associated with the bimodal (*sin2Θ*), positive value indicates a species' peak at pre-dawn and pre-dusk while the negative value indicates activity peak at post-dawn and post-dusk. With this approach, activity overlap between paired species was also tested through the construction of models representing the full 24-hour cycles (SinΘ, CosΘ, Sin2Θ, Cos2Θ). An ANOVA test was then conducted for each model to test for significant difference between species' activity of a pair, and the model with the highest adjusted R^2 was selected. This analysis was carried out in R program (R Core Team 2017).

In addition, Kernel density method was implemented to examine the difference in activity pattern between each pair of species (Ridout and Linkie 2009a). In the Kernel density approach, observed capture times are regarded as random samples from absolutely continuous underlying distributions, and a species' time of detection *t* is the proportion of hours and minutes in one day. A measure of overlap under this approach was calculated by fitting non-parametric kernel density functions to the species' diel activity data (Ridout and Linkie 2009a; Linkie and Ridout 2011), and was done using the package overlap_0.3.0 in R (Meredith and Ridout 2014). The coefficient of overlap (Δ) between the activity densities was calculated as a spectrum of proportional values, with 1 indicating complete overlap and 0 indicating no overlap. The non-parametric estimator Δ_4 was selected due to its superiority for sample sizes that are greater than 50 (Schmid and Schmidt 2006; Ridout and Linkie 2009a; Meredith and Ridout 2014). Following Lynam *et al.* (2013), value of $\Delta \geq 0.70$ and $\Delta < 0.35$ were defined as a high overlap

and a low overlap in diel activity, respectively. In addition to modeling activity overlap for the selected species pairs, an activity overlap of each selected carnivore species with each of their presumed principle prey species was also modeled.

Results

A total of 32,027 trap days were accumulated over 2013 - 2017 surveys across four study blocks (Table 1). Out of the five carnivore species, as we anticipated, the leopard cat had the highest number of independent photographs followed by the Asian golden cat (Table 2). The marbled cat on the other hand totalled the lowest number of independent events. Out of the three survey blocks where camera trapping was repeated three times, PD yielded the highest independent records for all felids but the lowest total of records for dhole (Table 2). Among the presumed prey species, the red muntjac *mutiacus muntjak* had the highest records in all blocks, followed by the stump-tailed macaque *Macaca arctoides*. Three out of four species of macaques detected during the study had less than 50 independent records, which were relatively low compared to those of all other prey species (Table 2).

Table 2: The number of independent records of felids and dhole, and presumed prey species from each survey block in Nam Et - Phou Louey National Protected Area during 2013 – 2017.

	Survey block			
Species	**NN**	**NPNV**	**PD**	**PS**
Asian golden cat *Catopuma temminckii*	8	53	73	38
Clouded leopard *Neofelis nebulosa*	5	34	56	52
Dhole *Cuon alpinus*	3	67	30	57
Leopard cat *Prionailurus bengalensis*	3	61	79	60
Marbled cat *Pardofelis marmorata*	2	45	47	31
Asian brush-tailed porcupine *Atherurus macrourus*	3	93	119	42
Assamese macaque *Macaca assamensis*	5	18	11	13
Small dark muntjac *M. rooseveltorum complex.*	2	206	210	36
East Asian porcupine *Hystrix brachyura*	17	136	167	70
Eurasian wild pig *Sus scrofa*	21	120	147	62
Grey peacock pheasant *Polyplectron bicalcaratum*	8	40	187	22
Indochinese serow *Capricornis milneedwardsii*	7	128	107	32
Pig-tailed macaque *Macaca leonina*	-	3	1	10
Red junglefowl *Gallus gallus*	7	18	105	17
Northern red muntjac *Muntiacus vaginalis*	83	489	629	292

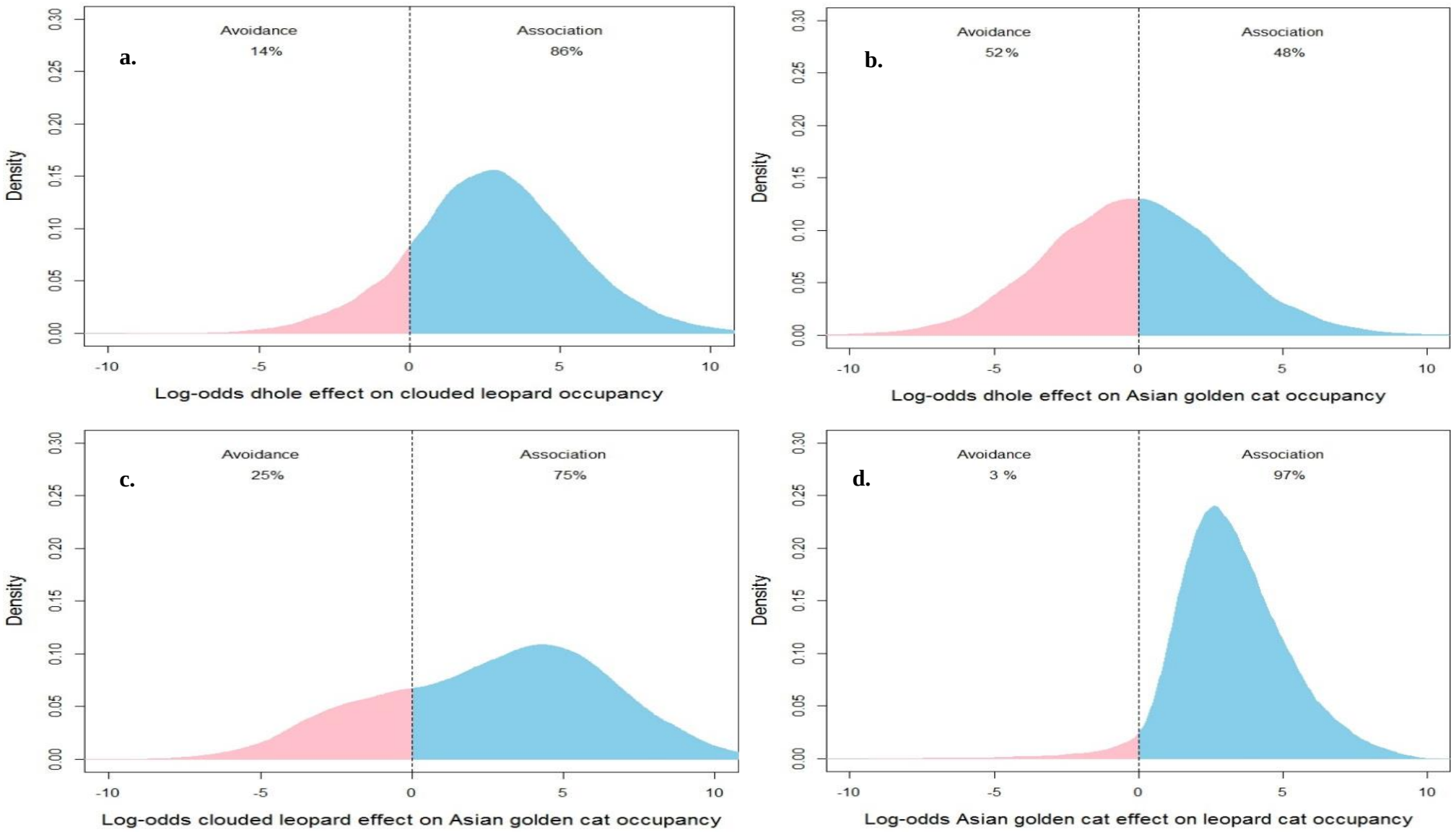
Red-cheeked squirrel *Dremomys rufigenis*	-	5	26	28
Rhesus macaque *Macaca mulatta*	5	6	13	15
Sambar *Cervus unicolor*	4	98	29	45
Silver pheasant *Lophura nycthemera*	12	81	74	59
Stump-tailed macaque *Macaca arctoides*	81	385	457	37
Bird spp.	3	66	73	49
Rat/Mice	8	78	134	191
Squirrel spp.	2	26	108	46

Occupancy model

Based on Gelman-Rubin diagnostics and the Rhat values from MCMC results (at convergence, Rhat = 1), all of our multi-species models converged, with R-hat values smaller than 1.05. Despite none of the estimated parameters indicating inter-specific effects on occupancy were significant (Table 3), the degree of association between species in the pairs of interest could still be interpreted. The final environmental covariates used for each species occupancy and detection are listed in Table 3 where the reported values of each species correspond to only those selected covariates.

Based on the comparison of the direction and extend of the posterior distribution deviation from 0 (Fig. 2), we found a little support for clouded leopard occupancy being influenced by dhole occupancy although there was a small sign of positive association between the species (Fig.2.a). Dhole occupancy did not appear to influence Asian golden cat occupancy (Fig.2.b). There was a slight evidence supporting the association between clouded leopard presence and Asian golden cat occupancy (Fig.2.c) while the leopard cat showed to be more likely to use the same sites as the Asian golden cat (Fig.2.d). Similarly, slight evidence suggested the marbled cat was

likely to share the same sites as the Asian golden cat (Fig.2.e). However, we found little support for marbled cat occupancy being influenced by the leopard cat presence although the coefficients for occupancy interaction effects tended to be positive, indicating moderate level of spatial overlap (Fig.2.f).


a.
Avoidance
14%
Association
86%
Density
Log-odds dhole effect on clouded leopard occupancy
b.
Avoidance
52%
Association
48%
Density
Log-odds dhole effect on Asian golden cat occupancy
c.
Avoidance
25%
Association
75%
Density
Log-odds clouded leopard effect on Asian golden cat occupancy
d.
Avoidance
3 %
Association
97%
Density
Log-odds Asian golden cat effect on leopard cat occupancy

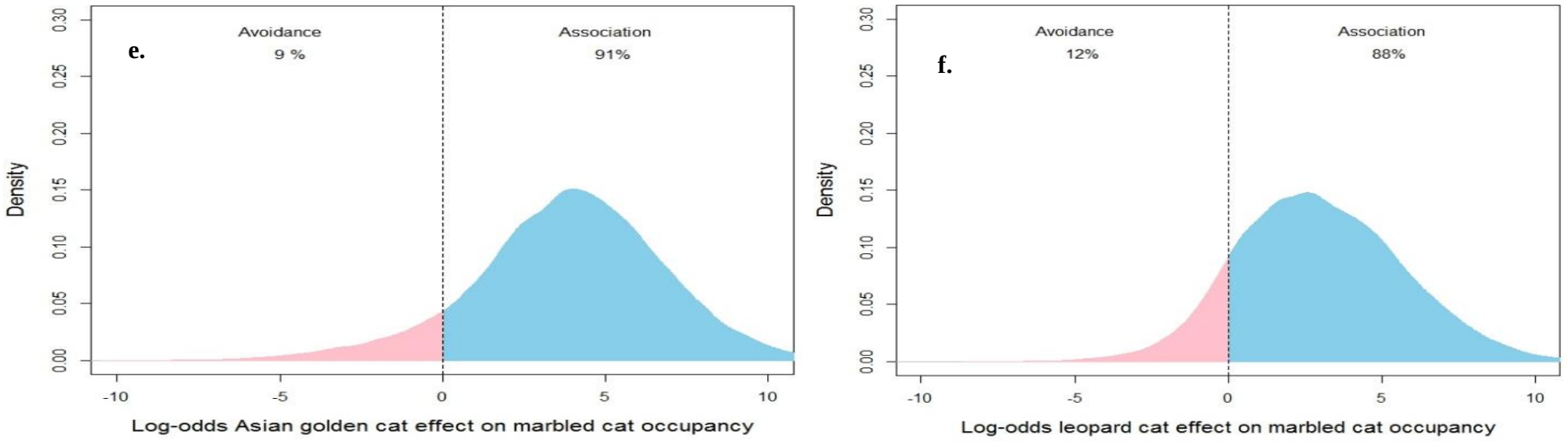


Fig.2: Results from Bayesian multi-species occupancy models evaluating spatial relationships between dhole, clouded leopard, Asian golden cat, leopard cat and marbled cat, based on the 2015/2016 camera trap survey data in Nam Et - Phou Louey National Protected Area. Plots associated with a given interaction show the distribution of the posterior probability of the estimated influence of one species' occupancy on that of another. The blue part indicates the probability of positive association and the pink part indicates probability of negative association/avoidance. Following Bischof *et al.* (2014), strongest evidence is associated with a model-predicted probability > 0.95

In terms of environmental factors affecting occupancy of targeted species (Table 3), we found that dhole occurrence was positively associated with density of settlement areas while avoiding mosaic areas. There was no evidence that any of the environmental/habitat covariates influenced clouded leopard occupancy. There was a slight evidence suggesting the Asian golden cat attraction to areas with high tree cover as well as grasslands. Similar to clouded leopard, the leopard cat and the marbled cat occupancy was not influenced by any of the habitat variables.

Table 3: Estimates of standardized regression coefficients ± standard deviation of factors affecting occupancy and detectability for felids and dhole, based on the 2016 camera trap survey data in Nam Et - Phou Louey National Protected Area. Estimates are given on the logit scale, with stars indicating significant effects. Significance was assessed using an approximation of the Wald statistic, defined as the coefficient divided by its standard error.

	D	**CL**	**AC**	**LC**	**MC**
Habitat factors for *psi()*	*C. alpinus*	*N. nebulosa*	*C. temminckii*	*P. bengalensis*	*P. marmorata*
Intercept	6.24 ± 2.36	1.61 ± 3.53	0.24 ± 4.19	-5.62 ± 2.53	-4.22 ± 4.02
Elevation	1.15 ± 2.18				
Prey encounter rate	-2.25 ± 1.97				
%Tree cover		1.49 ± 3.85	5.66 ± 3.17*		
Roughness		2.48 ± 2.84			-0.49 ± 3.03
Settlement density	6.99 ± 2.39**		1.49 ± 2.38		
% Agriculture					-1.35 ± 2.06
% Forest					0.55 ± 1.91
% Mosaic	-5.77 ± 2.32**		0.17 ± 2.22		
% Grassland		1.50 ± 4.29	6.47 ± 2.94*	-0.06 ± 0.26	

D presence		5.64 ± 3.08*	-1.17 ± 5.00		
CL presence			6.57 ± 3.59		
AC presence				5.01 ± 2.58**	6.88 ± 2.93*
LC Presence					5.91 ± 3.21*
Factors for detectability					
p0					
Intercept	-4.18 ± 0.25**	-3.29 ± 0.20**	-3.81 ± 0.25**	-1.62 ± 0.18**	-3.94 ± 0.31**
Prey encounter rate	0.61 ± 0.30*	0.06 ± 0.15	0.43 ± 0.12 **	0.43 ± 0.12**	0.62 ± 0.23*
Dhole presence		-0.13 ± 1.33	-4.72 ± 3.15*		
CL presence			-0.66 ± 1.31		
AC presence				0.00 ± 0.71	0.80 ± 0.92
LC Presence					0.04 ± 0.77

** represents strong evidence and * represents some evidence

Our detection model results showed no influence of dominant species on the subordinate species in most of the pairs, except that there was slight evidence suggesting that detection of the Asian golden cat was negatively affected by the presence of dhole (Table 3; Appendix 2). We found that dhole and marbled cat detections were slightly and positively influenced by prey encounter rate, while there was a strong evidence that detections of Asian golden cat and leopard cat were also positively affected by the same variables.

Circadian activity

There was strong evidence that activity patterns differ among the five-carnivore species (CosΘ*Species: F 95 = 14.78, $P < 0.001$; SinΘ*Species: F 95 = 3.22, $P = 0.01$). Dhole showed a strongly diurnal and crepuscular (both dawn and dusk) pattern of activity, with the highest peak of activity at dusk (Table 4 and Fig.3a). The clouded leopard was strongly crepuscular, but most active at dawn (Table 3 and Fig.3a). The Asian golden cat was active both by day and by night (Fig.3.b) but with a peak of activity at dawn (Table 4). The leopard cat was clearly nocturnal while the marbled cat was strongly diurnal with some activity at dawn and dusk (Table 4 and Fig.3f).

Table 4: Estimates of coefficients (± standard error) of diel activity models and best models with adjusted R^2 values for five carnivore species (D = dhole; CL = clouded leopard; AC = Asian golden cat; LC = leopard cat; MC = marbled cat). Significant values are marked with * where the most significant ones are marked with ***.

	SinΘ	**CosΘ**	**Sin2Θ**	**Cos2Θ**	**Best Model**	**Adjusted R2**
D	0.009 ± 0.005	-0.023 ± 0.005***	0.006 ± 0.005	-0.017 ± 0.005**	CosΘ + Cos2Θ	0.533
CL	0.035 ± 0.005***	0.006 ± 0.005	-0.004 ± 0.005	-0.021 ± 0.005***	SinΘ + Cos2Θ	0.737
AC	0.025 ± 0.006***	-0.002 ± 0.006	-0.003 ± 0.006	-0.002 ± 0.006	SinΘ	0.413
LC	0.008 ± 0.006	0.031 ± 0.006***	0.002 ± 0.006	-0.002 ± 0.006	CosΘ	0.495
MC	0.019± 0.008*	-0.030 ± 0.008***	-0.009 ± 0.008	-0.020 ± 0.008*	SinΘ + CosΘ + Cos2Θ	0.506

Diel activity overlaps between carnivores

The results from the activity difference modelling (i.e., wave analysis) showed that there was a difference in activity of species within each pair (the p-values of the best models of most pairs were < 0.05; Table 5). As for the extent of differences in their patterns of activity, the results from our kernel density activity overlap analysis were informative.

Table 5: Species pairing overlap estimates for kernel density (correlation coefficient *Δ4*), and significant wave(s) of best models for interaction between species pair.

Species pairing	Kernel density (*Δ4*)	Wave	Adjusted R2	p(t)
D/CL	0.51	SinΘ	0.525	0.009 (-2.919)
		CosΘ		0.046 (-2.145)
D/AC	0.66	SinΘ	0.604	0.010 (-2.874)
		CosΘ		0.046 (-2.144)
CL/AC	0.8	SinΘ	0.682	0.753 (-0.319)
		Cos2Θ		0.038 (-2.233)
AC/LC	0.55	SinΘ	0.722	0.044 (-2.161)
		CosΘ		<0.001 (4.992)
AC/MC	0.74	SinΘ	0.475	0.278 (-1.117)
		CosΘ		0.076 (-1.883)
LC/MC	0.31	CosΘ	0.366	0.002 (-3.540)
		Cos2Θ		0.372 (-0.915)

The activity overlap between dhole and clouded leopard (0.51 *Δ4*; Fig.3a) was slightly lower than that between dhole and Asian golden cat (0.66 *Δ4*; Fig.3b). Although our wave analysis suggested significant difference in Cos2Θ between clouded leopards and Asian golden cat, the SinΘ *p-value* was high (Table 5). This indicated a high level of overlap between the clouded

leopard and the Asian golden cat, a result consistent with the kernel density analysis which also indicated a strong overlap in. activity between them (0.80 *Δ4*; Fig.3c). We found that activity overlap between the Asian golden cat and the marbled cat was much higher than the overlap between the Asian golden cat and the leopard cat (0.74 *Δ4* and 0.55 *Δ4*; Fig.3e & d, respectively). Notably, the leopard cat and the marbled cat had the lowest overlap in activity (0.31 *Δ4*; Fig.3f).

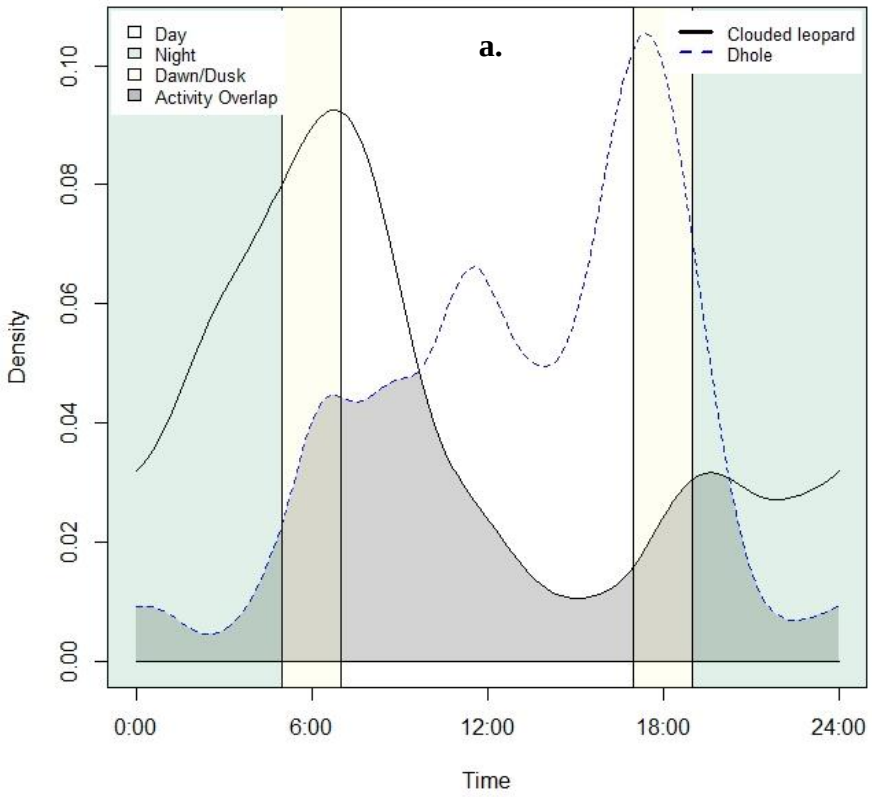
Diel activity overlap between carnivores and their prey

Six large- and medium-sized ungulate species have been identified as primary prey species for dhole – small dark muntjac(s) *M. rooseveltorum* complex, northern red muntjac *Mutiacus vaginalis*, sambar *Cervus unicolor*, Indochinese serow *Capricornis milneedwardsii*, and Eurasian wild pig *Sus scrofa* (Fig. S3.1). Dhole activity overlapped most strongly with the dark muntjac(s) (0.85 *Δ4*) and the Eurasian wild pig (0.80 *Δ4*). While both prey species were strongly diurnal, there was a peak of activity of the dark muntjac at dusk, closely corresponding to the behavior of the dhole (Fig. S3.1a).

A wide range of species have been considered as potential prey of clouded leopard, including large- and medium-sized angulates, four species of macaques, porcupines, squirrels, ground dwelling birds and other small birds (Fig. S3.2). Overall the overlap coefficients between the clouded leopard and these candidate prey species were greater than 0.40 *Δ4* (Fig. S3.2). The strongest overlaps were between the clouded leopard and the sambar deer and the mainland serow (0.79 *Δ4* and 0.75 *Δ4*, respectively). Clouded leopard overlapped particularly with prey species active at dawn.

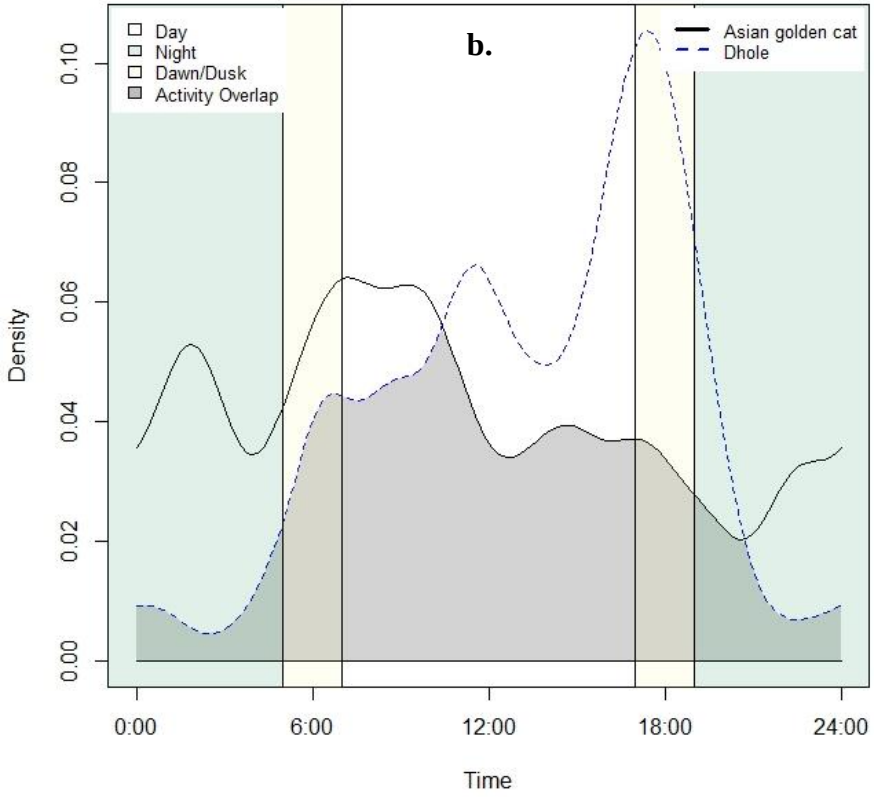
Dhole vs. Clouded leopard

(Δ4 = 0.51; CI: 0.39 - 0.57)



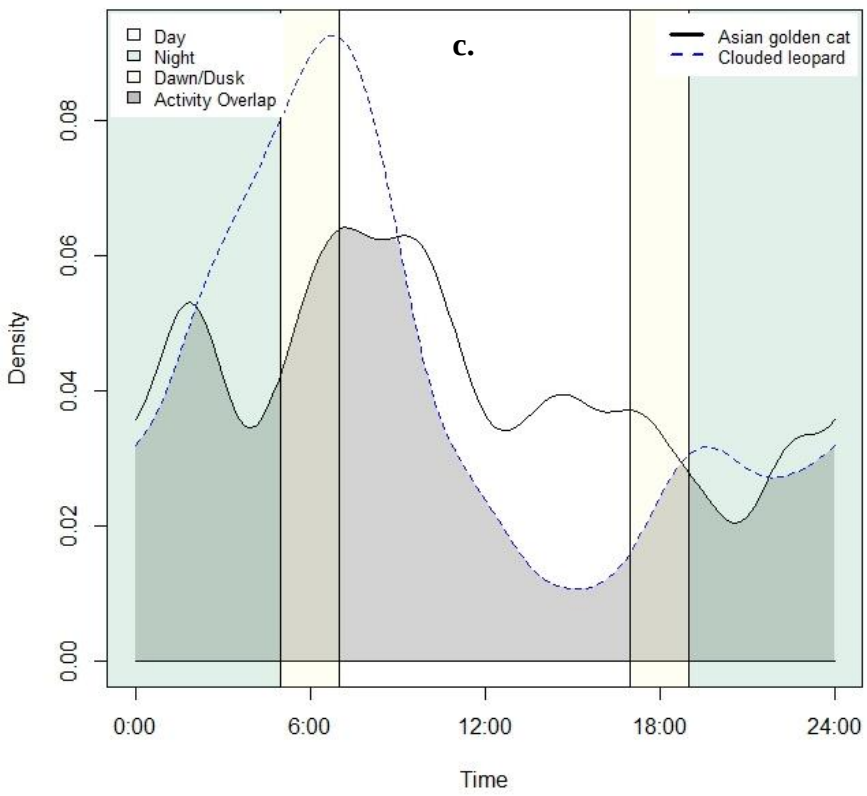
Dhole vs. Asian golden cat

(Δ4 = 0.66; CI: 0.55 - 0.74)



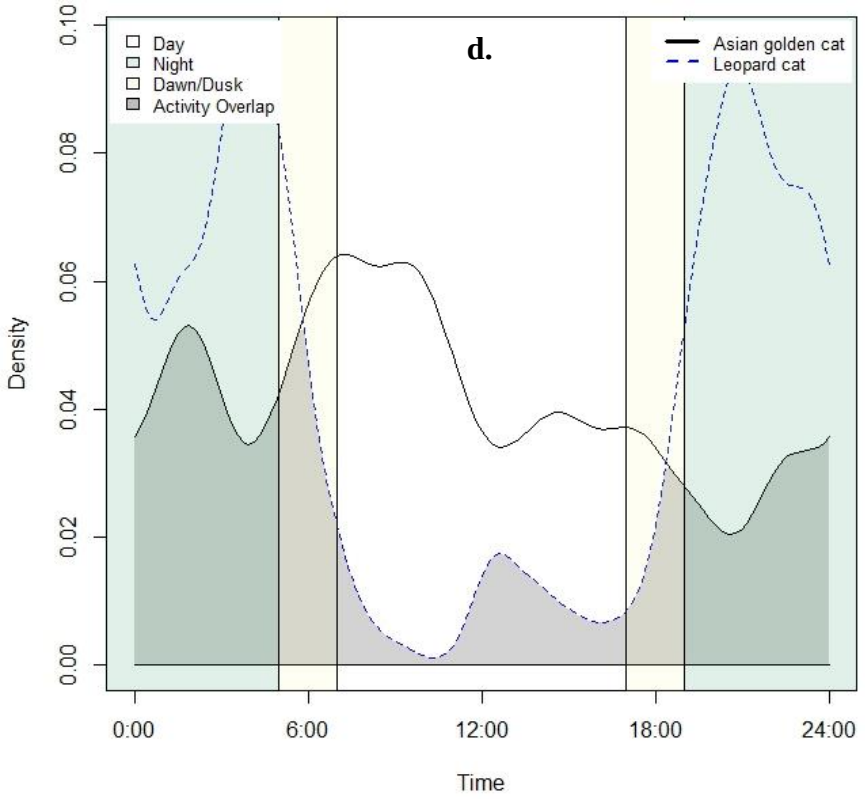
Clouded leopard vs. Asian golden cat

(Δ4 = 0.80; CI: 0.68 - 0.86)



Asian golden cat vs Leopard cat

(Δ4 = 0.55; CI: 0.43 - 0.60)



Asian golden cat vs. Marbled cat

(Δ4 = 0.74; CI: 0.65 - 0.81)

Leopard cat vs. Marbled cat

(Δ4 = 0.31; CI: 0.20 - 0.33)

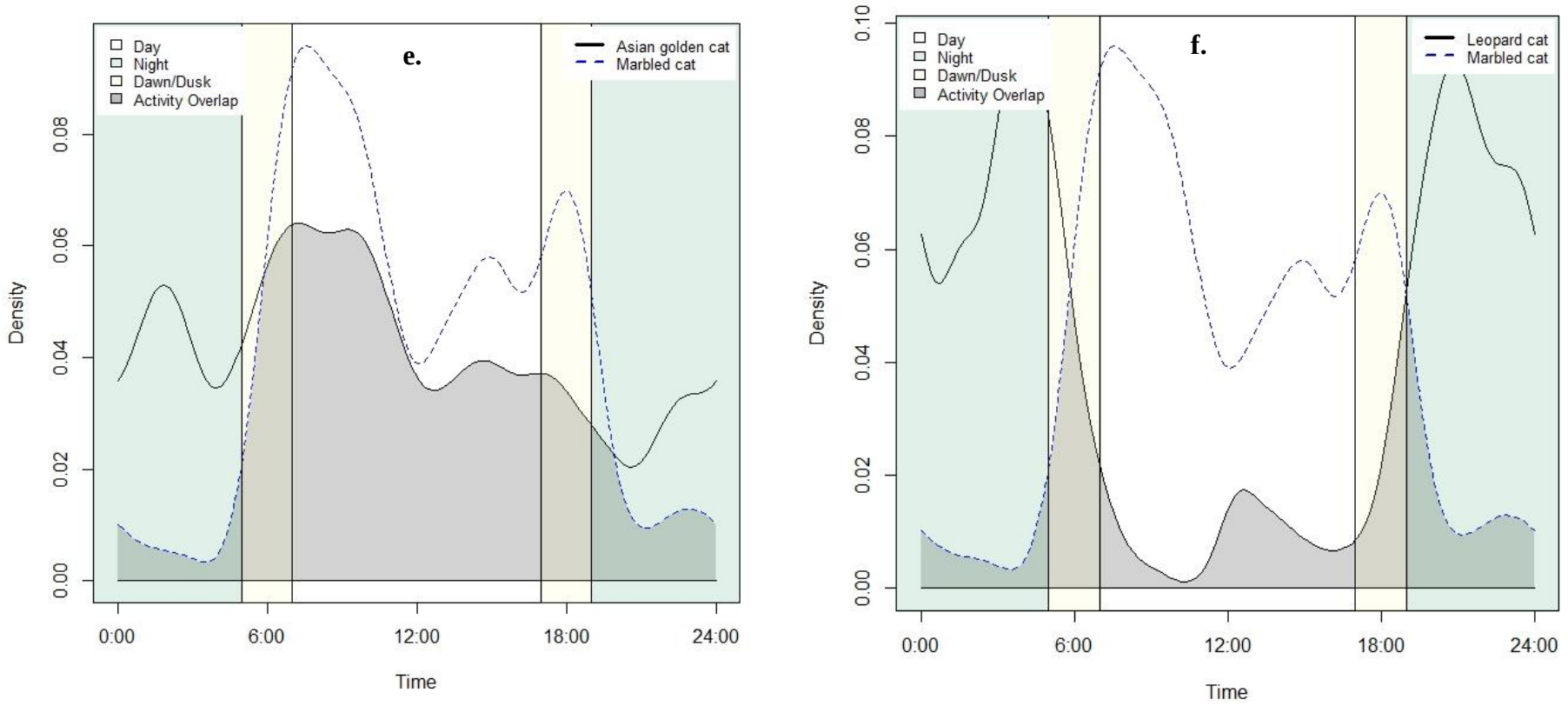


Fig. 3: Overlap in temporal activity between (a) dhole and clouded leopard, (b) dhole and Asian golden cat, (c) clouded leopard and Asian golden cat, (d) Asian golden cat and leopard cat, (e) Asian golden cat and marbled cat, (f) leopard cat and marbled cat in Nam Et - Phou Louey National Protected Area, Lao PDR, as measured by the kernel density across the 24-hour period.

Species identified as potential prey for the Asian golden cat included muntjac species, porcupines, squirrels, ground dwelling birds, other small birds and species of rat/mice. The golden cat's activity overlapped strongly with that of muntjacs, squirrels and all listed bird species (with overlap coefficients > 0.70 *Δ4*; Fig. S3.3) – these overlaps were more strongly congruent than those revealed for clouded leopard and their candidate prey species. Golden cat overlapped most fully with prey that were active by day, and they overlapped little with porcupines (0.45 *Δ4*) and species of rat/mice (0.42 *Δ4*).

The species thought to be prey of leopard cat and marbled cat are similar, including squirrels, bird species, and rats/mice. Insofar as rats/mice were strongly nocturnal they overlapped strongly with leopard cat (0.84 *Δ4*; Fig. S3.4f), but little with marbled cat which overlapped more strongly with candidate prey that were more diurnal (with overlap coefficients >0.70; Fig. S3.5a - e).

Discussion

Our investigation of felids and canids coexistence mechanisms provided some insights to verify our expectations. We acknowledged some limitations in our study, the more complete picture of resource partitioning could not be reached without a detailed investigation of species dietary behaviours. Nonetheless, our study provided a deeper insight into the spatial and temporal aspects of niche differentiation and highlighted an importance of camera trapping in studying illusive and low-density carnivores, especially for the NEPL.

Dhole and clouded leopard

Based on our pairwise niche segregation investigation. We found a small sign of positive spatial association between the clouded leopard and dhole which we could partially and conclusively say that our prediction (*P1*) was met. We anticipated such result because their diets largely overlap (Grassman *et al.* 2005a; Kamler *et al.* 2012; Selvan *et al.* 2013a; Selvan *et al.* 2013b).

It was not surprising that the clouded leopard somewhat showed to use the same sites as the dhole. This is because the latter is known for being a habitat generalist (Duckworth *et al.* 1999b), which would somehow lead to some degree of spatial overlap. However, there was a positive relationship between dhole and density of settlements and avoidance of mosaic areas while none of the environmental factors showed an influence on clouded leopard occupancy. For dhole, the attraction to human settlement area could only be explained by livestock predation. We suspect that this could be the case especially since numbers of large ungulates like gaur and sambar are relatively low, thereby causing dhole to perhaps move closer to livestock grazing areas for large prey. The species was reported as a major predators of large livestock (Duckworth *et al.* 1999b) and other studies also confirmed livestock (such as cattle and goats) represented part of dhole's diet (Cohen *et al.* 1978; Aryal *et al.* 2015). The study by Kamler *et al.* (2012) in NEPL showed that muntjacs (*Muntiacus*) and sambar (*Rusa unicolor*) were main prey species of dhole, which could also explain dhole's avoidance of mosaic area, because these prey species where shown to avoid areas with low levels of cover for their bed site locations (Brodie and Brockelman 2009). It was also suggested that thick vegetation could be more advantageous for dhole for stalk and ambush hunting techniques rather than cursorial hunting (Karwanishi and Sunquist 2008). While none of the habitat variables had a strong effect on the clouded leopard occupancy, the species seemed positively correlated with more tree cover, roughness and grassland. These findings are consistent with other studies suggesting their strong preference for forest habitats (Grassman *et al.* 2005a; Austin *et al.* 2007; Hearn *et al.* 2018b) while some were found to use more open habitat including grasslands (Nowell and Jackson 1996; Grassman *et al.* 2015). The positive association with roughness may explain two things – its association with serow *Capricornis milneedwardsii* occurrence and its mechanism to avoid direct encounter with dhole. Kamler *et al.* (2012) speculated that the fact that dhole is cursorial hunters and best adapted to pursuing prey on relatively flat terrain made them prey less on serow. Therefore, this type of prey specialisation might assist co-existence of dhole and

clouded leopard. Additionally, clouded leopard preys on primates (Nowell and Jackson 1996; Grassman *et al*. 2005a), whereas dhole was shown to not prey on primates in NEPL (Kamler *et al.* 2012). Therefore, differences in the distribution of primates within NEPL may also have influenced occupancy differences between clouded leopard and dhole.

The temporal activity overlap between dhole and clouded leopard was low, as predicted (*P1*). Dhole was mostly diurnal with a peak of activity at dusk, which is consistent with findings elsewhere (Cohen *et al.* 1978; Johnsingh 1992; Grassman *et al.* 2005b; Karwanishi and Sunquist 2008; Kumaraguru *et al.* 2011; Kamler *et al.* 2012; Bashir *et al.* 2014). Dhole activity strongly overlapped with that of dark muntjac(s) and Eurasian wild pig and with a moderate overlap with red muntjac, which are both primarily diurnal (Fig. S3.1) (Kawanishi and Sunquist 2004). There is a general question as to whether one would expect a prey's activity to coincide with that of its predators, or vice versa, but insofar as the former is the case we note that muntjacs and wild pig have been recorded as prey of dhole by Kamler *et al.* (2012) in NEPL and Wang and Macdonald (2009) in Bhutan. However, studies elsewhere suggest that the sambar is the most, and the wild pig is the least, preferred prey of dhole (Cohen *et al.* 1978; Venkataraman *et al.* 1995; Karwanishi and Sunquist 2008; Wang and Macdonald 2009; Thinley *et al.* 2011; Kamler *et al.* 2012; Hayward *et al.* 2014), we found much less congruence in the predator's activity with sambar than with wild pig.

The clouded leopard was crepuscular with a peak at dawn, as observed in Thailand (Austin *et al.* 2007) but not elsewhere (Azlan and Sharma 2006; Lynam *et al.* 2013; Gumal *et al.* 2014; Sunarto *et al.* 2015). In NEPL clouded leopard activity synchronised with that of the mainland serow and sambar (Fig. S3.2). The extent to which clouded leopards may synchronise with their prey or seek to avoid the activity of dholes is unknown.

Dhole and Asian golden cat

Our prediction that the Asian golden cat avoided dhole spatially but not temporally (*P2*) contrasted with our findings. The Asian golden cat occupancy was not affected by dhole presence. Their occurrences were independent of one another. This could be that the Asian golden cat is also a habitat generalist (Dhendup 2016). We found the species was positively associated with both open and closed habitat which supports the previous speculation of habitat generalisation and is consistent with previous studies (Wang (2007b); Lyngdoh *et al.* (2011). The Asian golden cat was shown to be crepuscular with activities intensified from dawn until midmorning. Based on the kernel density activity plot (Fig.3.b), the species seemed to be active both day and night which is also consistent with other studies from NEPL (Johnson *et al.* 2009), Thailand (Lynam *et al.* 2013), Malaysia (Azlan and Sharma 2006; Karwanishi and Sunquist 2008), and Bhutan (Jigme 2011; Thinley *et al.* 2015; Vernes *et al.* 2015).

The Asian golden cat was crepuscular with activity intensified from dawn until midmorning. Based on the kernel density activity plot (Fig.3.b), the species seemed to be active both day and night, which is consistent with other studies from NEPL (Johnson *et al.* 2009), Thailand (Lynam *et al.* 2013), Malaysia (Azlan and Sharma 2006; Karwanishi and Sunquist 2008), and Bhutan (Jigme 2011; Thinley *et al.* 2015; Vernes *et al.* 2015). Its temporal overlap with dhole was moderate, contrary to the expectation of *P2*; most of that overlap was during daylight. Given the moderate overlap with dhole and a strong overlap with small-sized prey species (Fig. S3.3), one might hypothesise that the Asian golden cat preys particularly on squirrels and birds, taking small ungulates opportunistically. According to Grassman *et al.* (2005a), small mammals (< 2.5kg) constituted 78% of Asian golden cat's diet. Cathemerality may enable the Asian golden cat to fit flexibly into the SE Asian felid and canid guild.

Clouded leopard and Asian golden cat

Despite the similarity in size between the clouded leopard and the Asian golden cat, the morphological difference of the clouded leopard in terms of the canine size (Nowell and

Jackson 1996; Sunquist and Sunquist 2002) would give it a dominant position over the Asian golden cat. As such we predicted the Asian golden cat to spatially and temporally avoid the clouded leopard. Our findings did not support this prediction (*P3*). The species interaction modelling results showed a slight positive association, which indicated a small degree of habitat overlap between the two species.

Despite the similarity in size between the clouded leopard and the Asian golden cat, the morphological difference of the clouded leopard in terms of the canine size (Nowell and Jackson 1996; Sunquist and Sunquist 2002) distinguishes these felids. We had predicted the Asian golden cat would temporally avoid the clouded leopard (*P3*), but this was not upheld – the two species were active at similar times and most especially at dawn. This accords with observations of Sunda clouded leopard, *Neofelis diardi*, in Sumatra by McCarthy *et al.* (2015b), who speculated that the species were separated by the clouded leopard's greater arboreality. However, another study in Sumatra by Haidir *et al.* (2018) found temporal differentiation between the Sunda clouded leopard and the Asian golden without evidence of spatial avoidance between the species. This was more consistent to our prediction.

Asian golden cat and small felids

It appeared that the marbled cat did not avoid the Asian golden cat as we originally thought (*P4*), as the association was positive, suggesting coexistence between the two species. However, our findings that there was a significant positive association between the Asian golden cat and the leopard cat supported our initial prediction (*P4*). Looking at how strongly both marbled cat and leopard cat associated with Asian golden cat occurrence, we would have thought that the same habitat factors of the Asian golden cat would explain the occupancy of the two small felids, but none of the factors were shown to strongly influence their occurrence. This could be that the presence of the Asian golden cat was the most highly influential variable compared to others in the models. With such positive association between the Asian golden cat and the leopard cat, we infer that the leopard cat occurs in the same type of habitat as the Asian golden

cat, which includes both open and closed habitat types. This conclusion is supported by previous studies in Laos (Duckworth *et al.* 1999b; Johnson *et al.* 2009), Thailand (Grassman *et al.* 2005a; Lynam *et al.* 2013), and Borneo (Mathai *et al.* 2010; Mohamed *et al.* 2013a; Mohamed *et al.* 2016; Hearn *et al.* 2018b).

The fact that our results show a slightly lower strength of association between the Asian golden cat and the marbled cat, compared to that of the Asian golden cat and the leopard cat, suggests a slight difference in marbled cat habitat use. It could be that the marbled cat specialised more on forest habitats as previously reported (Macdonald and Loveridge 2010).

While a study in Thailand found that leopard cat and marbled cat had similar levels of temporal overlap with the Asian golden cat (Lynam *et al.* 2013), in NEPL we found that Asian golden cat activity patterns overlap more with that of the marbled cat than with that of the leopard cat, in accord with our prediction (*P4*). We found that the marbled cat in NEPL was primarily diurnal which is consistent with findings of studies from the NEPL (Johnson *et al.* 2009), Thailand (Lynam *et al.* 2013), Sumatra (Sunarto *et al.* 2015) and India (Singh and Macdonald 2017). In contrast, Grassman *et al.* (2005a) found a single radio-collared animal was nocturnal. In NEPL the activity of marbled cat coincided with that of avian and arboreal prey (Grassman *et al.* 2005a). It seems that marbled cat and Asian golden cat are likely to have different dietary specialities.

In accord with studies elsewhere (Grassman 2000; Grassman *et al.* 2005c; Austin *et al.* 2007; Johnson *et al.* 2009; Lynam *et al.* 2013; Singh and Macdonald 2017), we found leopard cat in NEPL was strongly nocturnal. Several studies, including ours, suggested that its activity is adapted to coincide with murid prey (Fig.S3.4f) (Rajaratnam 2000; Roll *et al.* 2006; Rajaratnam *et al.* 2007b; Cheyne and Macdonald 2011). Clearly there is temporal differentiation between leopard cat and Asian golden cat.

Leopard cat and marbled cat

At NEPL there was little overlap in circadian activity between the leopard cat and the marbled cat, as we expected (*P5*). This accords with other studies (Lynam *et al.* 2013; Singh and Macdonald 2017). One might expect that species more similar in body size, will overlap less in other dimensions of resource utilisation. Our results, and those of Lynam *et al.* (2013) and Sunarto *et al.* (2015) appear to support this expectation. Considering their activity patterns, and those of their candidate prey, it seems likely that marbled cat and leopard cat coexist by eating different prey and by being active at different times.

Conclusion

Our study is one of the few detailed studies available in the region (Grassman 2004; Karwanishi and Sunquist 2008; Lynam *et al.* 2013; Sunarto *et al.* 2015) that looked at not only felid but also canid communities to capture a fuller picture of interspecific interactions. This is also the first detailed study that provided insights into the ecology of felid and canid communities in the NEPL as well as in the whole of Laos. For the species about which so little is known, such as the Asian golden cat and marbled cat, our findings add to the pool of knowledge and understanding of their ecology which are important for their conservation, especially since most of these species are listed as Threatened or Near Threatened by the IUCN. Our findings in terms of factors influencing species spatial distribution can further be used to produce predictive map that can benefit conservation planning.

We are aware of a number of the limitations of this study. The lack of dietary analysis component may have weakened our inference slightly. Inference from this study for small cat species might be limited because our survey was designed to target the clouded leopard or carnivores of similar size. That said, we are confident that the records we obtained for small felids adequately represented their ecology. Nonetheless, our camera trapping design did not

consider arboreal activities of clouded leopard and marbled cat, although it is not clear if arboreal and terrestrial activity would differ for these species. Moreover, all habitat covariates used in our occupancy modelling were extracted based on a single scale, which could be the reason why we could not find evidence of habitat association for some of our targeted species.

Future research should consider extracting covariates in multiple scales for each species because scales are important for understanding ecological patterns and processes (Kre *et al.* 2009; Razgour *et al.* 2011). While some species distribution may be explained by a large scaled landscape patterns, smaller scaled habitat patterns may explain the distribution of others better. We believe that seasonal interactions should be investigated, as our study could be bias towards only what happened during the dry season, because the species may have different level of interactions depending on seasonal change in resource availability (Boyer *et al.* 2003). Nonetheless, our results clearly illustrate the mechanisms by which species coexist within a diverse community of felids and a canid in the evergreen and semi-evergreen forests of northern Lao PDR.

Authors' contributions

A.R., conceived the ideas, designed methodology, collected and analysed the data within a wider regional study of clouded leopards conceived and led by DWM, interpreted analysis results and led the writing of the manuscript. J.K., D.W.M, supervised the research, checked the manuscript contents and references. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank the Wildlife Conservation Society and the Nam Et- Phou Louey National Protected Area for their extensive in-kind support. We further thank Mr. Phonesouk Chanthalavong for

his assistance and Dr. Lucy Talents for her guidance. We deeply grateful for the Exploration Grant from the National Geographic and a grant to DWM from the Robertson Foundation.

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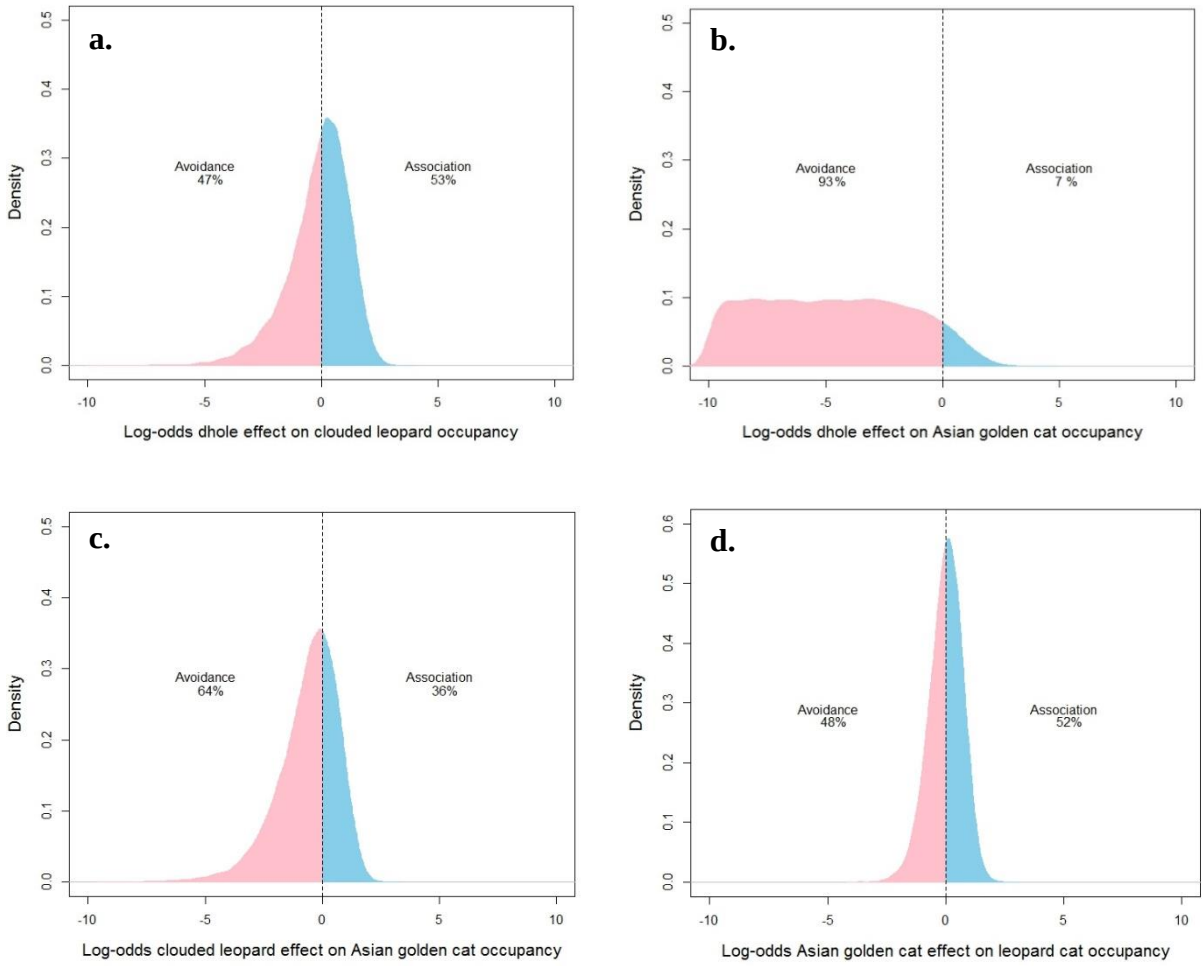
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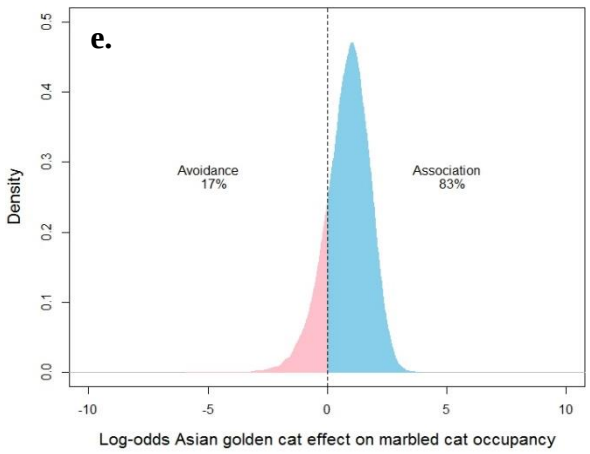
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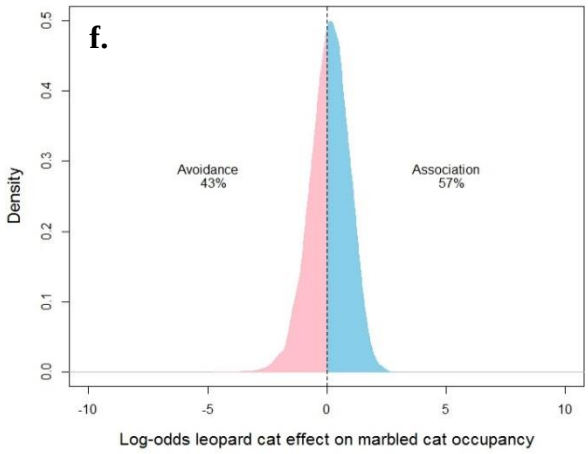
Appendix S1: Habitat covariates, metrics calculated, and data sources. Focal mean and standard deviation (SD) were calculated for all continuous variables. PLAND (percentage of landscape) was calculated for categorical variables.

Covariate	Metric	Data source
Elevation	Focal mean & SD	Jarvis *et al.* 2008 (http://srtm.csi.cgiar.org)
% Forest cover	Focal mean & SD	Hansen *et al.* 2013 (http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.2.html)
Settlement density	Focal mean & SD	Lao National Geographic Department
Roughness	Focal mean & SD	Evans *et al.* 2014 (ArcGIS Geomorphometry & Gradient Metrics Toolbox; http://evansmurphy.wixsite.com/evansspatial/arcgis-gradient-metrics-toolbox)
Land cover classes: agricultural, Forest, grassland and mosaic	PLAND, GYR, CWED	ESA CCI Land Cover layer 300m 2015 (www.esa-landcover-cci.org/?q=node/175); Nam Et - Phou Louey National Protected Area land cover layer 30m 2015 by the Wildlife Conservation Society Lao PDR.

Appendix S2: Results from Bayesian multi-species occupancy models evaluating spatial relationships between dhole, clouded leopard, Asian golden cat, leopard cat and marbled cat, based on the 2016 camera trap survey data in Nam Et - Phou Louey National Protected Area. Plots associated with a given interaction show the distribution of the posterior probability of the estimated influence of one species' occupancy on detection of another. The blue part indicates the probability of positive association and the pink part indicates probability of negative association/avoidance. Following Bischof *et al.* (2014), strongest evidence is associated with a model-predicted probability > 0.95.

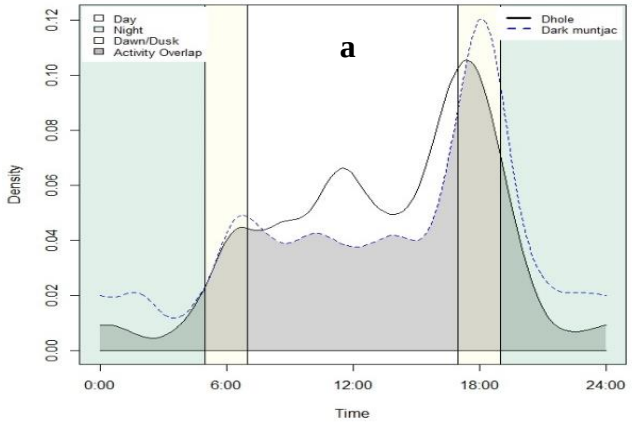



e.
Density
Avoidance
17%
Association
83%
0.0
0.1
0.2
0.3
0.4
0.5
-10
-5
0
5
10
Log-odds Asian golden cat effect on marbled cat occupancy

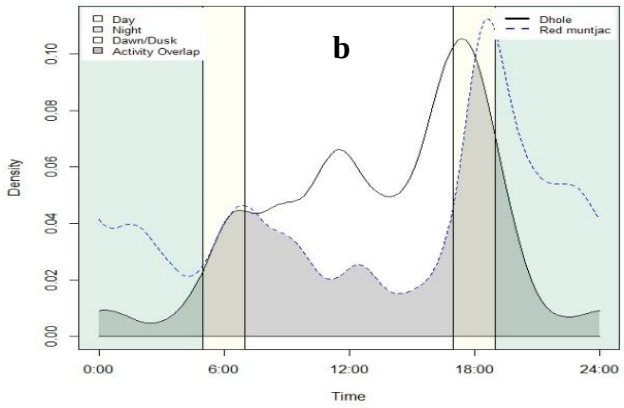

f.
Density
Avoidance
43%
Association
57%
0.0
0.1
0.2
0.3
0.4
0.5
-10
-5
0
5
10
Log-odds leopard cat effect on marbled cat occupancy

Appendix S3: Activity overlaps between carnivores and their presumed prey species.

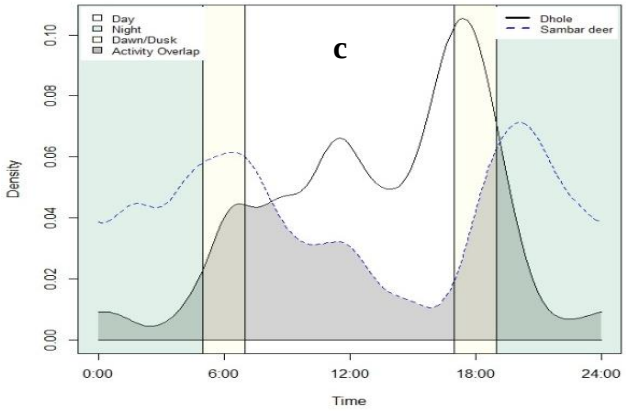
Dhole cat vs. Dark muntjac
Δ4 = 0.85 (CI: 0.71; 0.89)



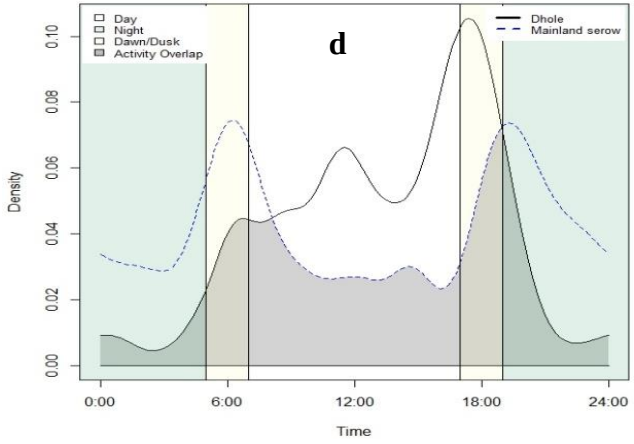
Dhole cat vs. Red muntjac
Δ4 = 0.65 (CI: 0.52; 0.67)



Dhole cat vs. Sambar
Δ4 = 0.57 (CI: 0.46; 0.64)



Dhole cat vs. Serow
Δ4 = 0.63 (CI: 0.47; 0.67)



Dhole cat vs. Eurasian wild pig
Δ4 = 0.80 (CI: 0.67; 0.85)

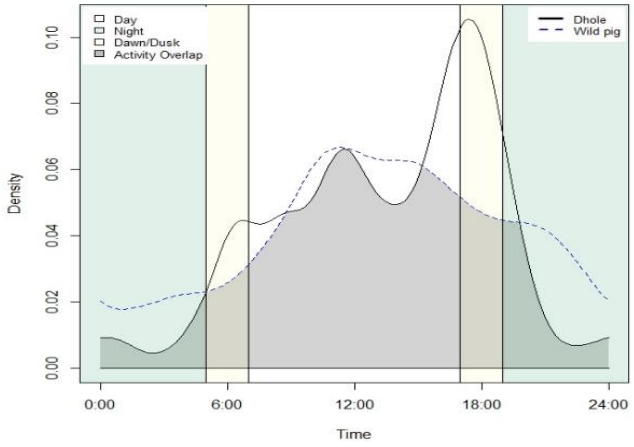
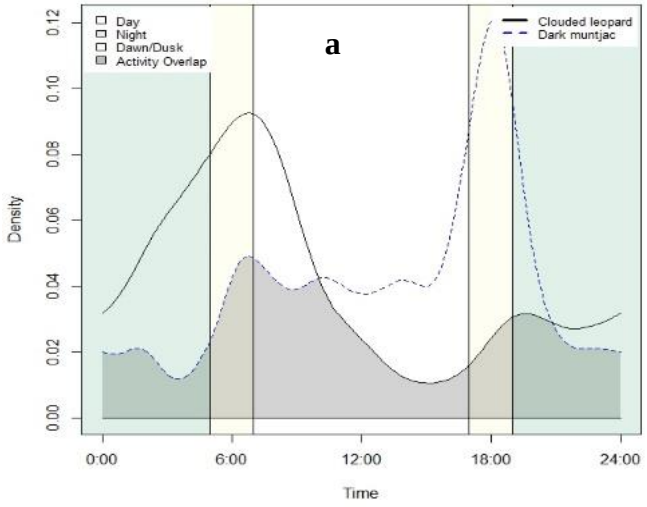
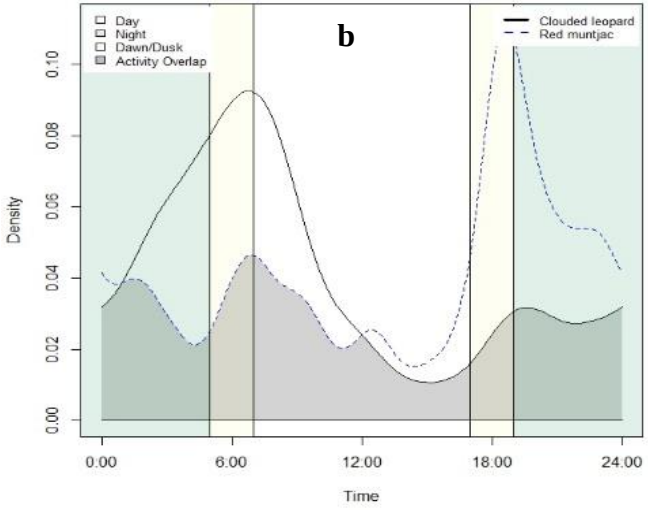


Fig.S3.1. Diel activity overlaps between dholes (*Cuon alpinus*) and prey species.

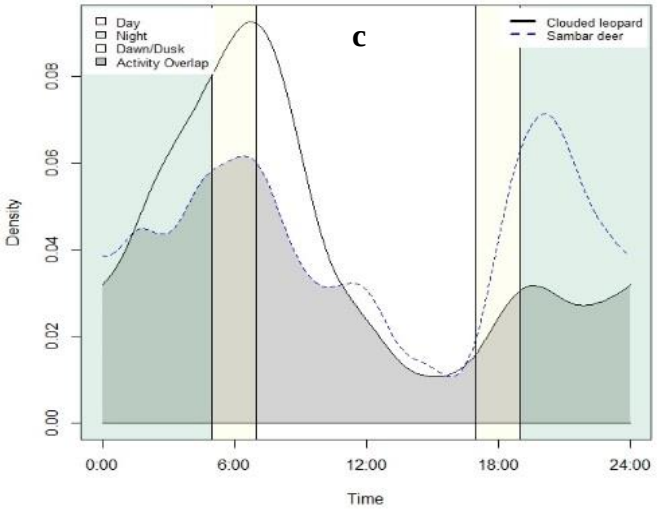
Clouded leopard vs. Dark muntjac
Δ4 = 0.60 (CI: 0.51 ; 0.66)



Clouded leopard vs. Red muntjac
Δ4 = 0.65 (CI: 0.57; 0.71)

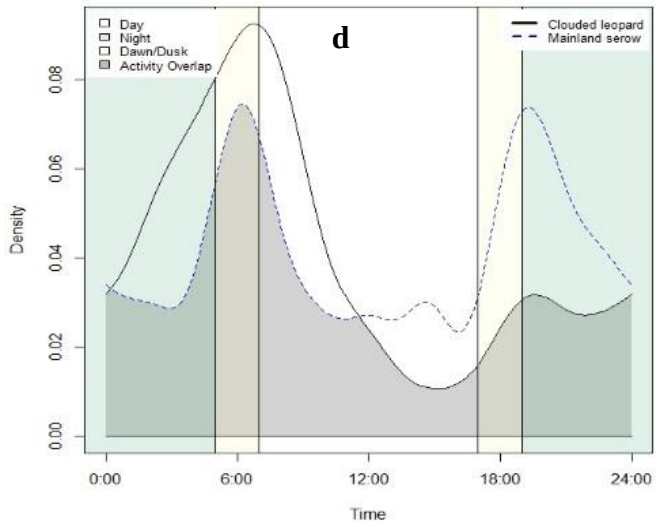


Clouded leopard vs. Sambar
Δ4 = 0.79 (CI: 0.69; 0.87)



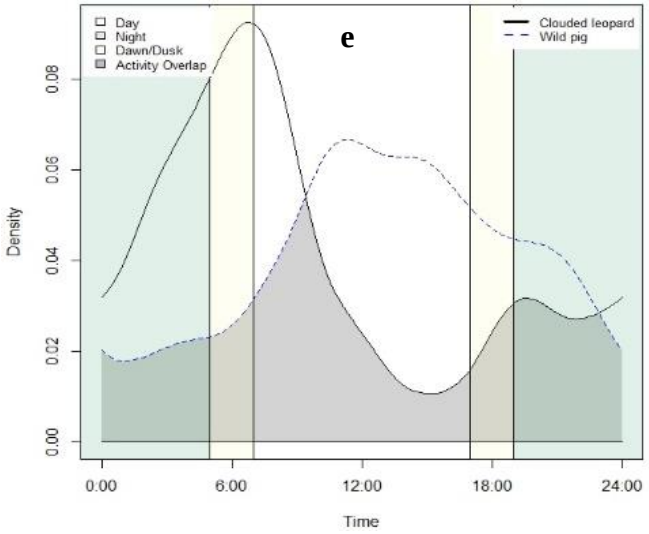
Clouded leopard vs. Serow

Δ4 = 0.75 (CI: 0.64; 0.82)



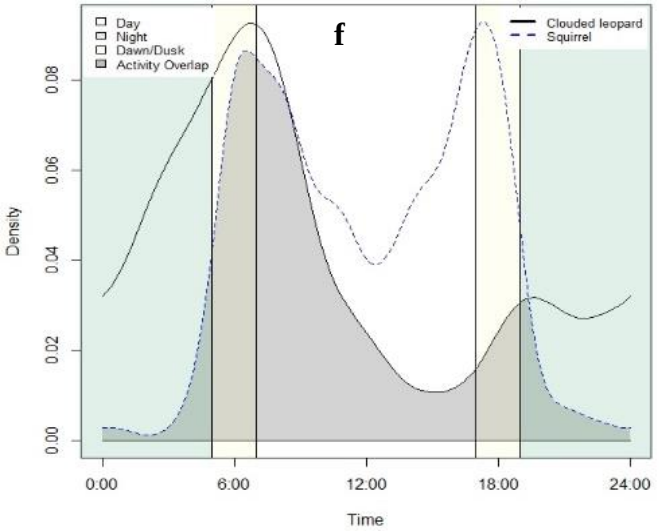
Clouded leopard vs. Eurasian wild pig

Δ4 = 0.60 (CI: 0.48; 0.64)



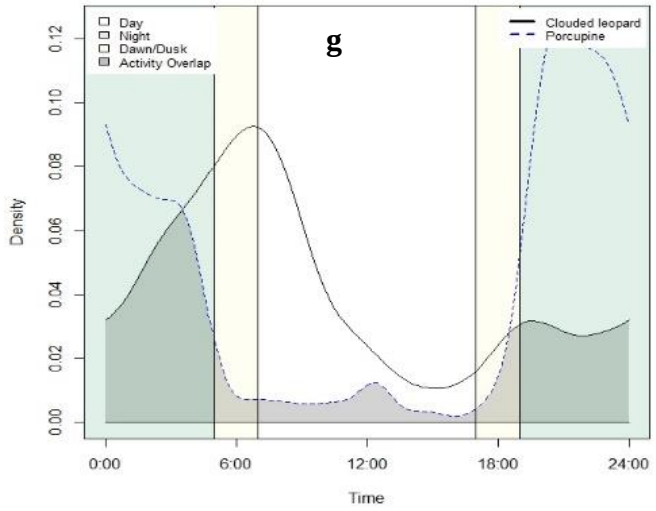
Clouded leopard vs. Squirrels

Δ4 = 0.63 (CI: 0.54; 0.70)



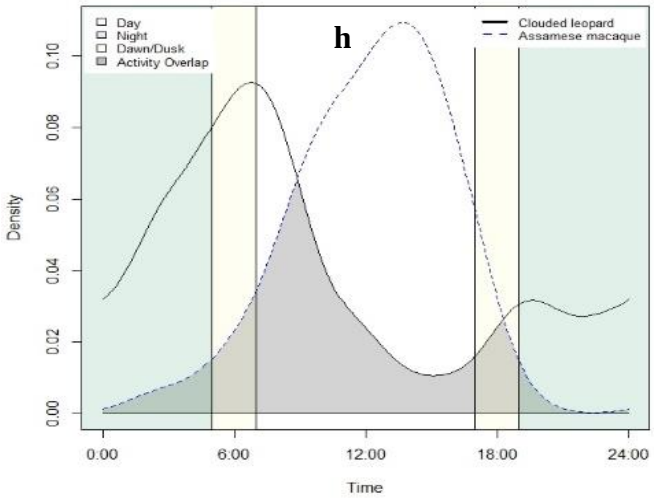
Clouded leopard vs. Porcupines

Δ4 = 0.50 (CI: 0.42; 0.56)



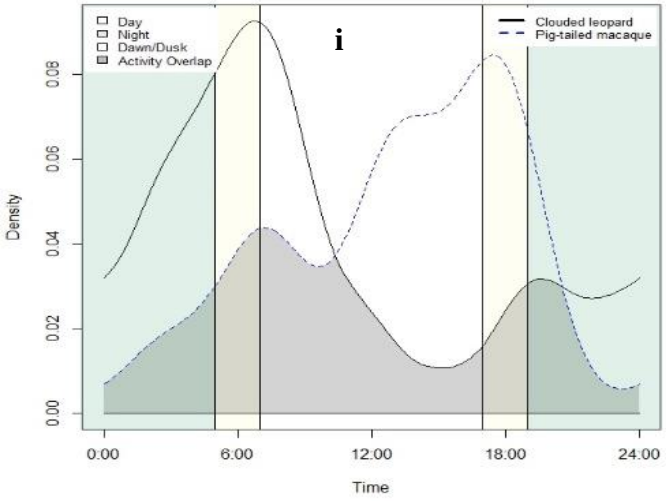
Clouded leopard vs. Assamese macaque

Δ4 = 0.41 (CI: 0.24; 0.46)

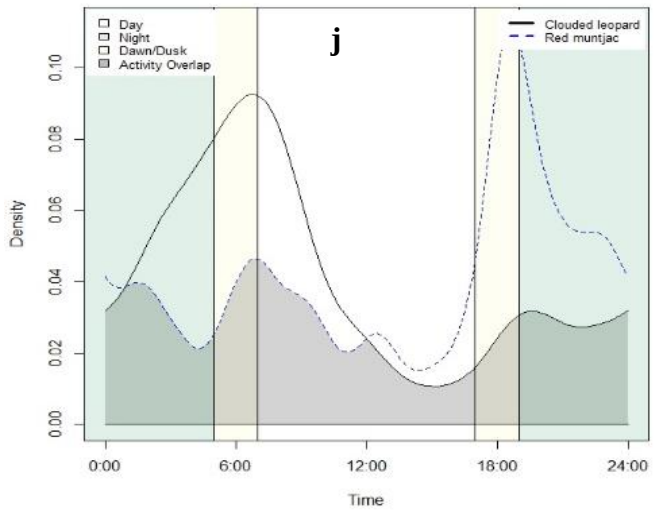


Clouded leopard vs. Pig-tailed macaque

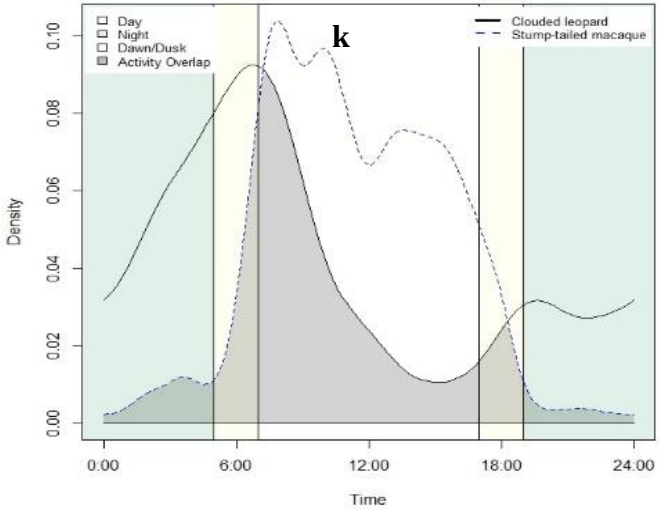
Δ4 = 0.51 (CI: 0.27; 0.71)



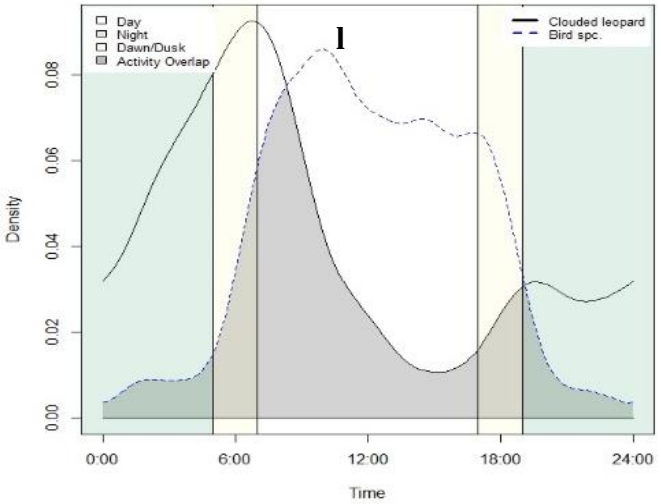
Clouded leopard vs. Rhesus macaque
Δ4 = 0.42 (CI: 0.25; 0.49)



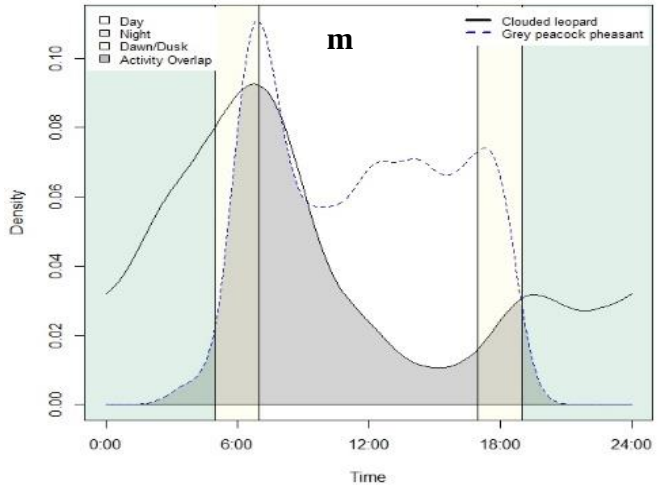
Clouded leopard vs. Stump-tailed macaque
Δ4 = 0.52 (CI: 0.43; 0.57)



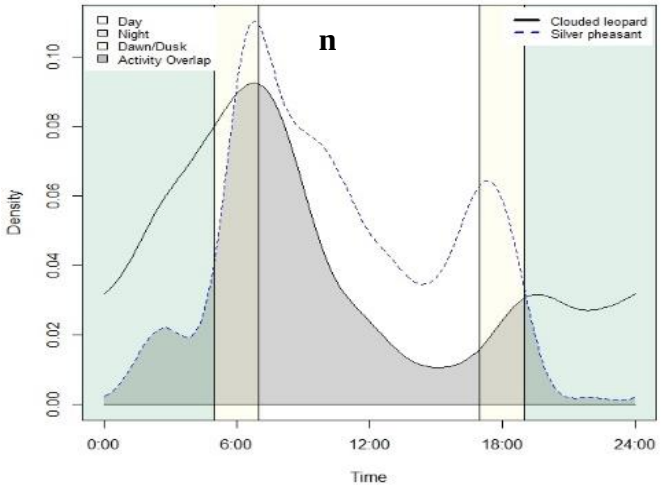
Clouded leopard vs. Birds
Δ4 = 0.53 (CI: 0.43; 0.59)



Clouded leopard vs. Grey peacock pheasant
Δ4 = 0.56 (CI: 0.47; 0.62)



Clouded leopard vs. Silver pheasant
Δ4 = 0.67 (CI: 0.57; 0.74)



Clouded leopard vs. Red junglefowl
Δ4 = 61 (CI: 0.49; 0.66)

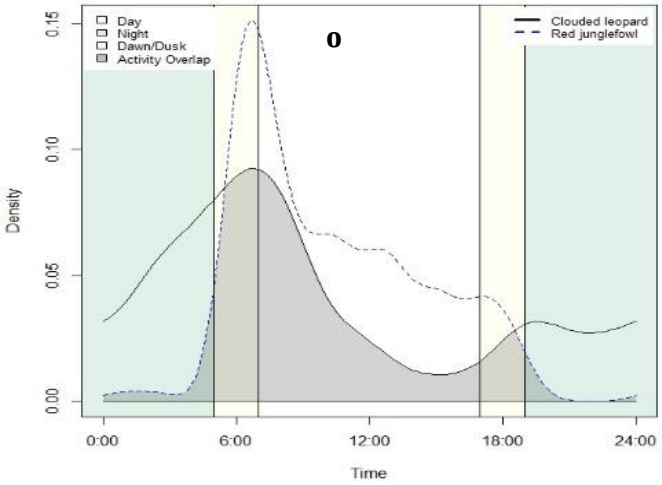
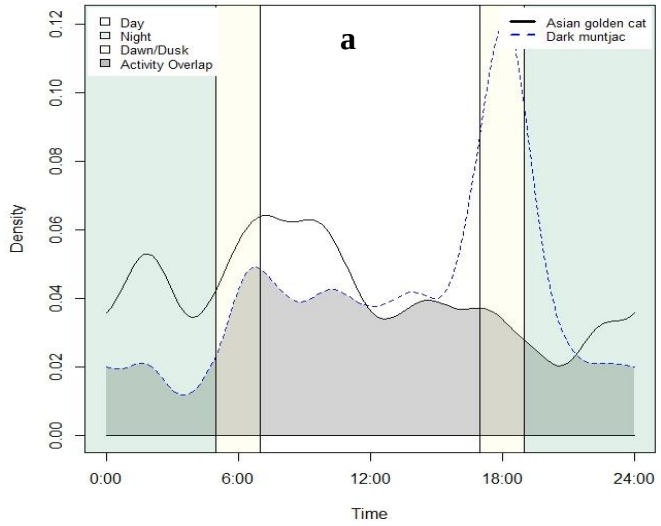


Fig.S3.2. Diel activity overlaps between clouded leopards (*Neofelis nebulosa*) and prey species.

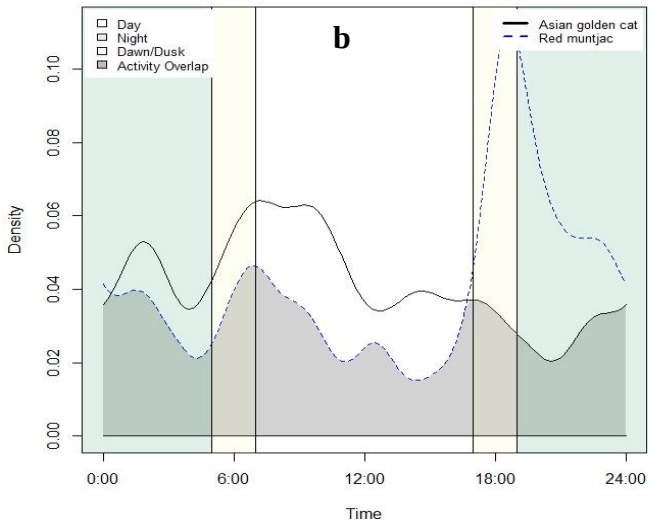
Asian golden cat vs. Dark muntjac

Δ4 = 0.73 (CI: 0.65 ; 0.80)



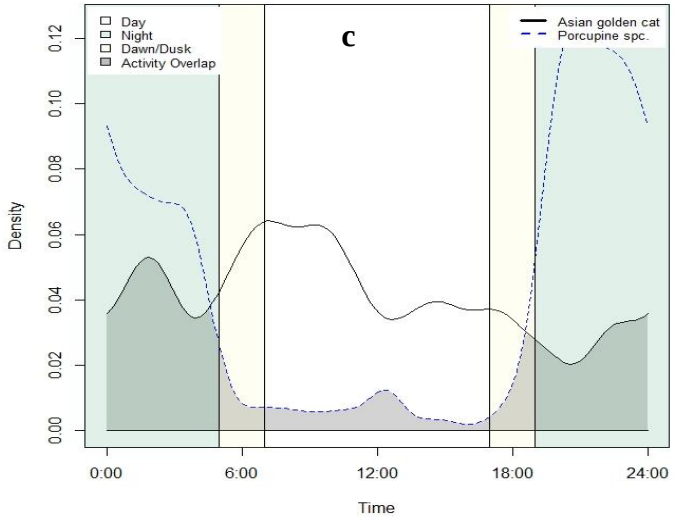
Asian golden cat vs. Red muntjac

Δ4 = 0.70 (CI: 0.62; 0.75)



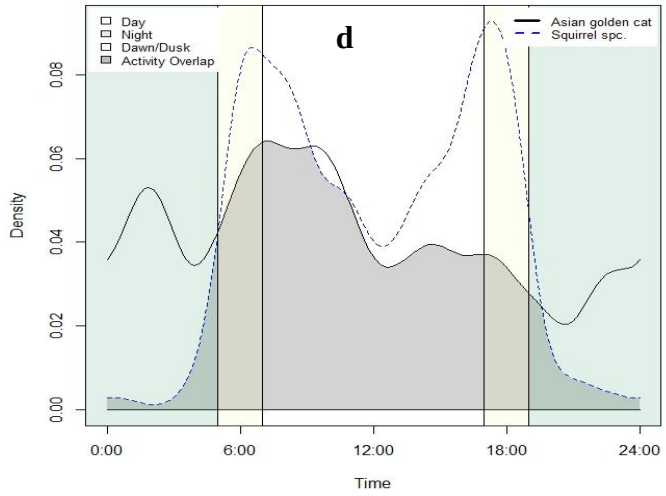
Asian golden cat vs. Porcupines

Δ4 = 0.45 (CI: 0.35; 0.48)



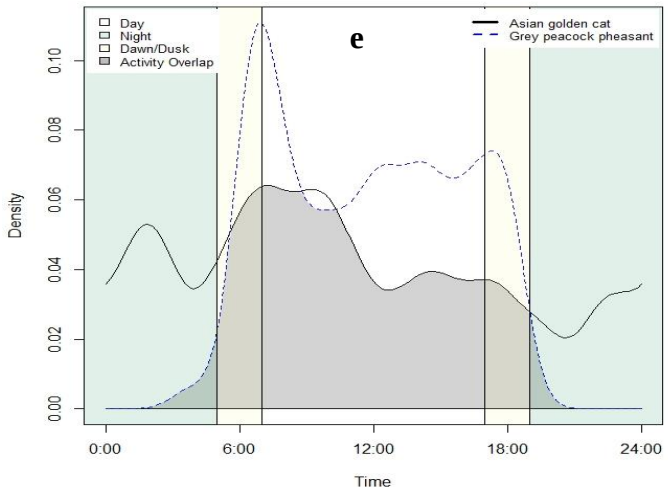
Asian golden cat vs. Squirrels

Δ4 = 0.72 (CI: 0.64; 0.78)



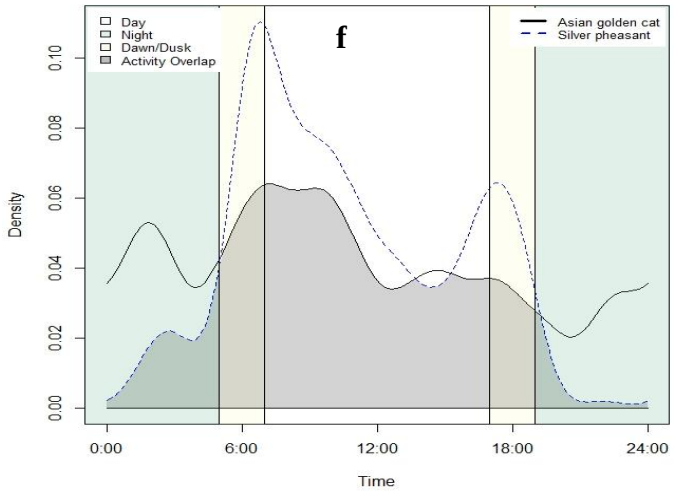
Asian golden cat vs. Grey peacock pheasant

Δ4 = 0.66 (CI: 0.57; 0.71)



Asian golden cat vs. Silver pheasant

Δ4 = 0.75 (CI: 0.66; 0.81)



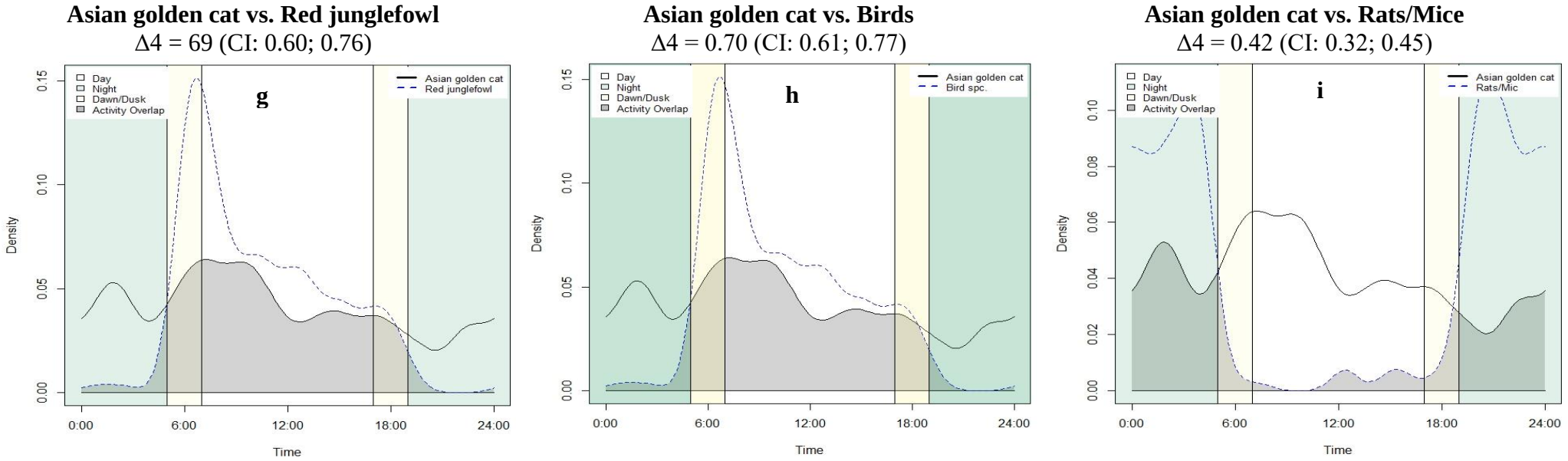


Fig.S3.3. Diel activity overlaps between Asian golden cats (*Catopuma temminckii*) and prey species.

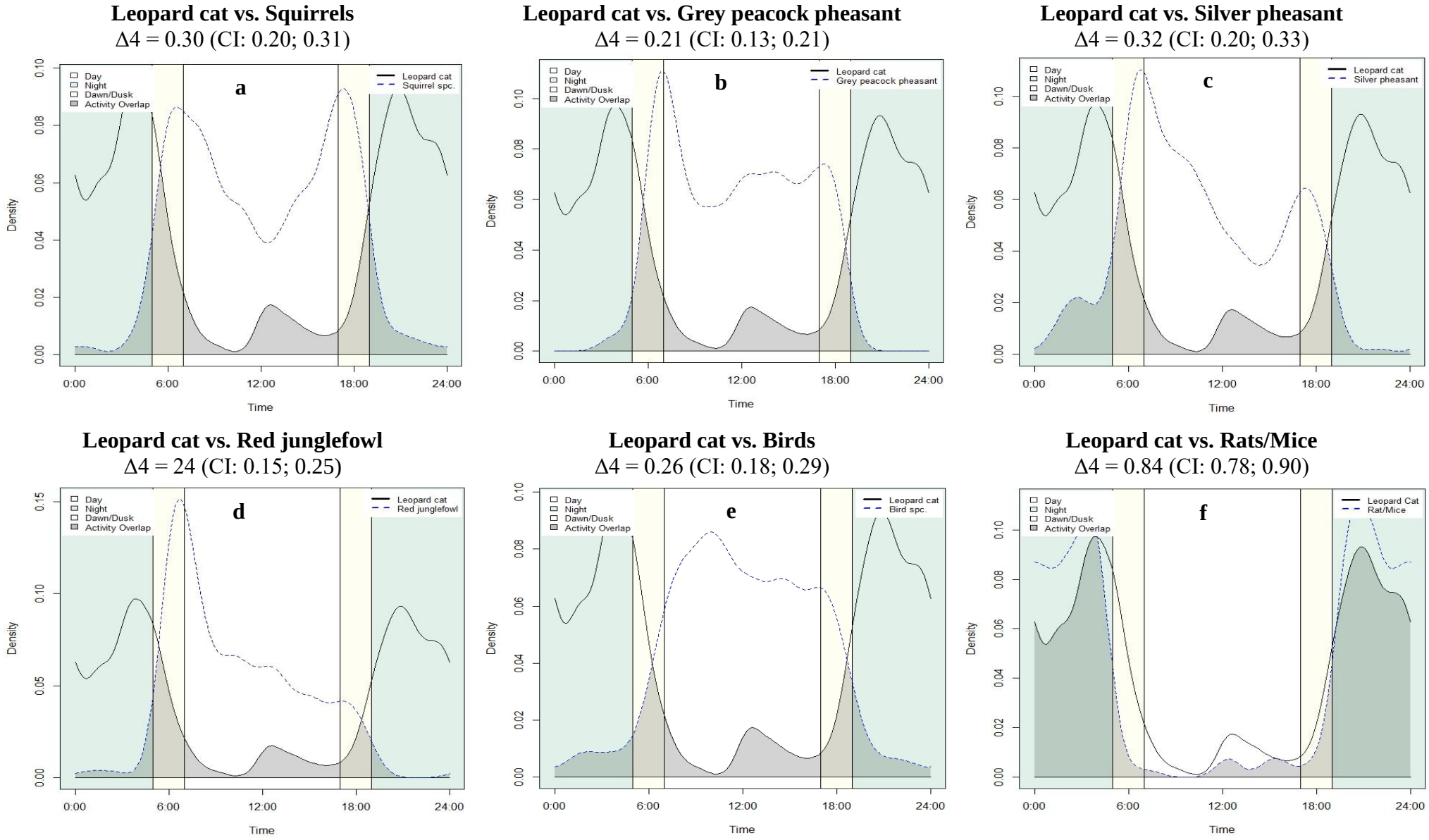
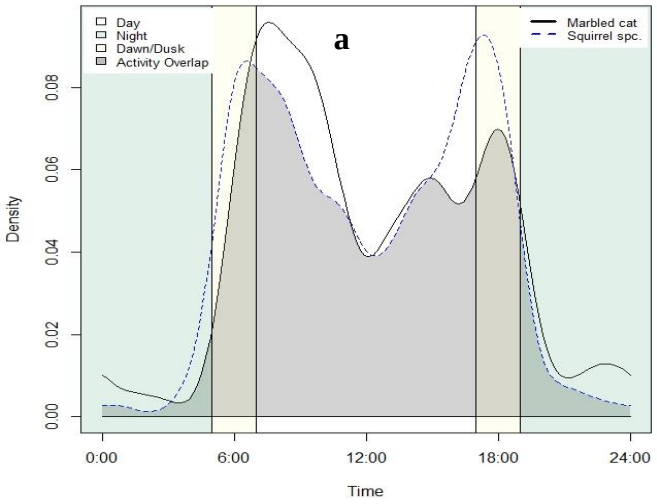
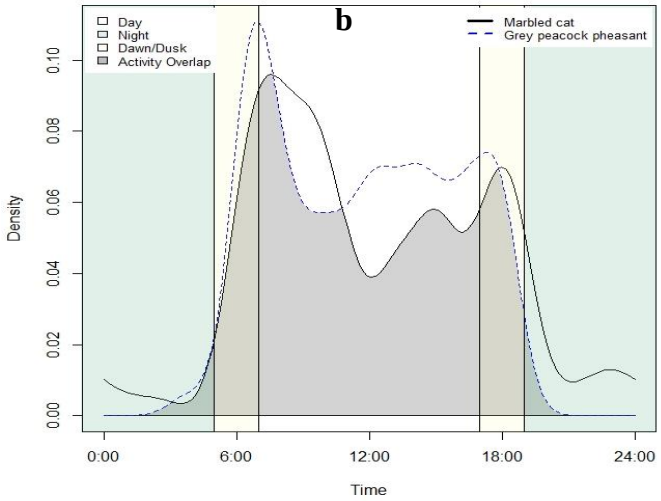


Fig.S3.4. Diel activity overlaps between leopard cats (*Prionailurus bengalensis*) and prey species.

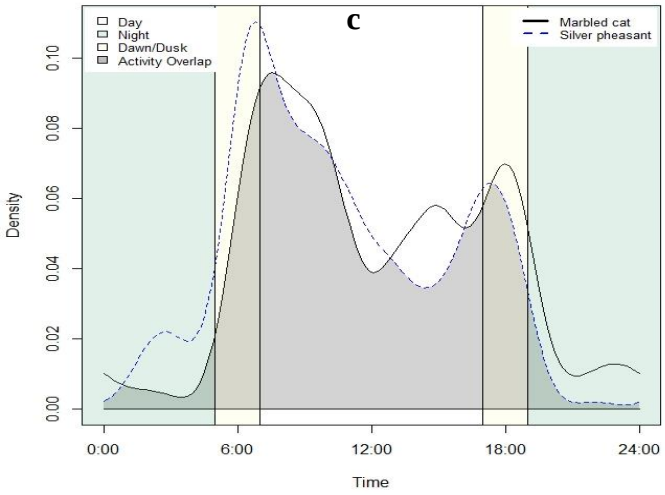
Marbled cat vs. Squirrels
Δ4 = 0.88 (CI: 0.83; 0.94)



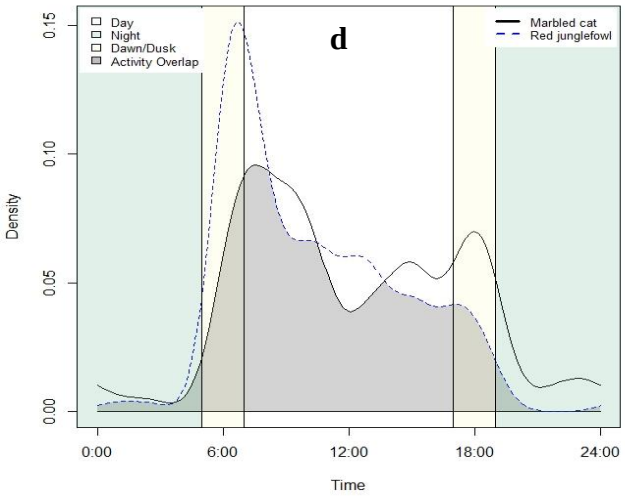
Marbled cat vs. Grey peacock pheasant
Δ4 = 0.84 (CI: 0.75; 0.90)



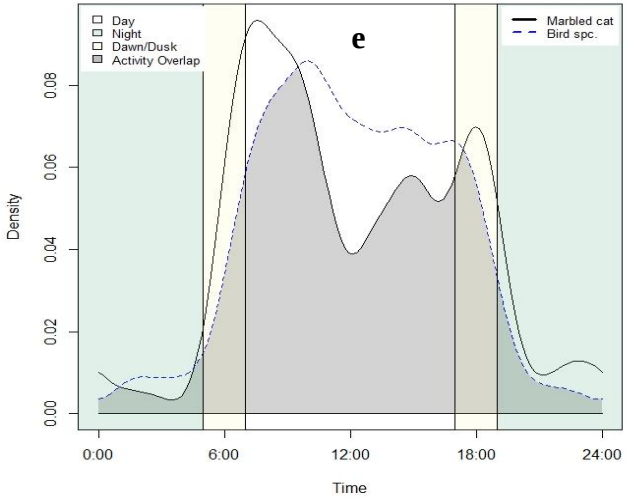
Marbled cat vs. Silver pheasant
Δ4 = 0.86 (CI: 0.80; 0.92)



Marbled cat vs. Red junglefowl
Δ4 = 79 (CI: 0.70; 0.87)



Marbled cat vs. Birds
Δ4 = 0.84 (CI: 0.76; 0.91)



Marbled cat vs. Rats/Mice
Δ4 = 0.17 (CI: 0.10; 0.17)

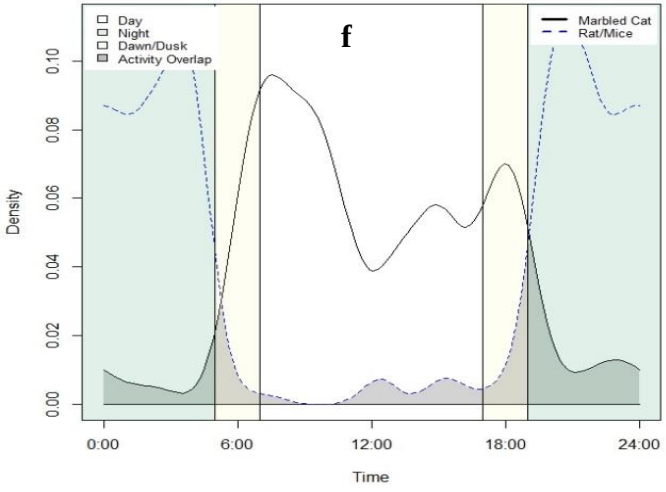


Fig.S3.5. Diel activity overlap between marbled cats (*Pardofelis marmorata*) and prey species.

Appendix S4: JAGS Code for Multi-Species Interactions Model

```
model{
#-----------------------------------------------------------------
# ------------------PRIORS FOR INTERCEPT PARAMETERS-----------
#-----------------------------------------------------------------
    # Dhole
    a.psi.D ~ dunif(-10,10)
    a.p.D ~ dunif(-10,10)

    # Clouded leopard
    a.psi.CL ~ dunif(-10,10)
    a.p.CL ~ dunif(-10,10)

    # Asian Golden cat
    a.psi.AC ~ dunif(-10,10)
    a.p.AC ~ dunif(-10,10)

    # Leopard cat
    a.psi.LC ~ dunif(-10,10)
    a.p.LC ~ dunif(-10,10)

    # Marbled cat
    a.psi.MC ~ dunif(-10,10)
    a.p.MC ~ dunif(-10,10)

#-----------------------------------------------------------------
# ------------------PRIORS FOR INTER-SPECIFIC PARAMETERS------
#-----------------------------------------------------------------
# Dhole - Clouded leopard
   b.psi.D.CL ~ dnorm(0, 0.1)  # dhole on clouded leopard psi

   b.p.D.CL ~ dunif(-10,10)  # dhole on clouded leopard p

# Dhole - Asian Golden cat
    b.psi.D.AC ~ dnorm(0, 0.1)     # dhole on golden cat psi
    b.p.D.AC ~ dunif(-10,10)       # dhole on golden cat p

# Clauded leopard - Asian Golden cat
    b.psi.CL.AC ~ dnorm(0, 0.1)
    b.p.CL.AC ~ dunif(-10,10)

# Asian golden cat - Leopard cat
    b.psi.AC.LC ~ dnorm(0, 0.1)
    b.p.AC.LC ~ dunif(-10,10)

# Golden cat - Marbled cat
    b.psi.AC.MC ~ dnorm(0, 0.1)
    b.p.AC.MC ~ dunif(-10,10)
```

```
# Leopard cat - Marbled cat
    b.psi.LC.MC ~ dnorm(0, 0.1)
    b.p.LC.MC ~ dunif(-10,10)

#-----------------------------------------------------------------
# ------------------ PRIORS FOR COVARIATE EFFECTS ------------
#-----------------------------------------------------------------
# Occupancy
    #-Dhole
    b.elev.psi.D ~ dunif(-10,10)          # Elevation
    b.prey.psi.D ~ dunif(-10,10)          # Prey RAI
    b.TC.psi.D ~ dunif(-10,10)            # TC = tree cover
    b.rough.psi.D ~ dunif(-10,10)         # Roughness
    b.VillDens.psi.D ~ dunif(-10,10)      # Vill density
    b.agric.psi.D ~ dunif(-10,10)         # Agriculture
    b.forest.psi.D ~ dunif(-10,10)         # Forest
    b.mosaic.psi.D ~ dunif(-10,10)         # Mosaic area
    b.grass.psi.D ~ dunif(-10,10)         # Grass-shrub

    #------Clouded leopard
    b.elev.psi.CL ~ dunif(-10,10)          # Elevation
    b.prey.psi.CL ~ dunif(-10,10)          # Prey RAI
    b.TC.psi.CL ~ dunif(-10,10)            # TC = tree cover
    b.rough.psi.CL ~ dunif(-10,10)         # Roughness
    b.VillDens.psi.CL ~ dunif(-10,10)      # Vill density
    b.agric.psi.CL ~ dunif(-10,10)         # Agriculture
    b.forest.psi.CL ~ dunif(-10,10)         # Forest
    b.mosaic.psi.CL ~ dunif(-10,10)         # Mosaic area
    b.grass.psi.CL ~ dunif(-10,10)         # Grass-shrub

   #------Asian Golden cat
    b.elev.psi.AC ~ dunif(-10,10)          # Elevation
    b.prey.psi.AC ~ dunif(-10,10)          # Prey RAI
    b.TC.psi.AC ~ dunif(-10,10)            # TC = tree cover
    b.rough.psi.AC ~ dunif(-10,10)         # Roughness
    b.VillDens.psi.AC ~ dunif(-10,10)      # Vill density
    b.agric.psi.AC ~ dunif(-10,10)         # Agriculture
    b.forest.psi.AC ~ dunif(-10,10)         # Forest
    b.mosaic.psi.AC ~ dunif(-10,10)         # Mosaic area
    b.grass.psi.AC ~ dunif(-10,10)         # Grass-shrub

    #------Leopard cat
    b.elev.psi.LC ~ dunif(-10,10)          # Elevation
    b.prey.psi.LC ~ dunif(-10,10)          # Prey RAI
    b.TC.psi.LC ~ dunif(-10,10)            # TC = tree cover
    b.rough.psi.LC ~ dunif(-10,10)         # Roughness
    b.VillDens.psi.LC ~ dunif(-10,10)      # Vill density
    b.agric.psi.LC ~ dunif(-10,10)         # Agriculture
    b.forest.psi.LC ~ dunif(-10,10)         # Forest
    b.mosaic.psi.LC ~ dunif(-10,10)         # Mosaic area
```

```
    b.grass.psi.LC ~ dunif(-10,10)       # Grass-shrub

    #------Marbled cat
    b.elev.psi.MC ~ dunif(-10,10)        # Elevation
    b.prey.psi.MC ~ dunif(-10,10)        # Prey RAI
    b.TC.psi.MC ~ dunif(-10,10)          # TC = tree cover
    b.rough.psi.MC ~ dunif(-10,10)       # Roughness
    b.VillDens.psi.MC ~ dunif(-10,10)    # Vill density
    b.agric.psi.MC ~ dunif(-10,10)       # Agriculture
    b.forest.psi.MC ~ dunif(-10,10)       # Forest
    b.mosaic.psi.MC ~ dunif(-10,10)       # Mosaic area
    b.grass.psi.MC ~ dunif(-10,10)       # Grass-shrub

 ###################
 # Detection
    #------Dhole
    b.prey.p.D ~ dunif(-10,10)    # Prey RAI

    #------Clouded leopard
    b.prey.p.CL ~ dunif(-10,10)    # Prey RAI

    #------Asian golden cat
    b.prey.p.AC ~ dunif(-10,10)    # Prey RAI

    #------Leopard cat
    b.prey.p.LC ~ dunif(-10,10)    # Prey RAI

    #------Marbled cat
    b.prey.p.MC ~ dunif(-10,10)    # Prey RAI

#-------------------------------------------------------------
#------------------LIKELIHOODS--------------------------------
#-------------------------------------------------------------
#- OCCUPANCY
    for (i in 1:n) {
     z.D[i] ~ dbern(psi.D[i])

    #+++++++++++++++ Dhole  ++++++++++++++++++++++++++
logit(psi.D[i]) <- a.psi.D + b.elev.psi.D * elev[i] +
b.prey.psi.D * D.prey[i] + b.TC.psi.D * TC[i] +
b.VillDens.psi.D * villdens[i] + b.rough.psi.D * rough[i] +
b.agric.psi.D * agric[i] + b.forest.psi.D * forest[i] +
b.mosaic.psi.D * mosaic[i] + b.grass.psi.D * grass[i]
                  }
    #-------------------------------------------------------
    for (i in 1:n) {

     z.CL[i] ~ dbern(psi.CL[i])

    #++++++++++++ Clouded leopard (affected by dhole)+++++++
```

```
logit(psi.CL[i]) <- a.psi.CL + b.elev.psi.CL * elev[i] +
b.prey.psi.CL * CL.prey[i] + b.TC.psi.CL * TC[i] +
b.VillDens.psi.CL * villdens[i] + b.rough.psi.CL * rough[i] +
b.agric.psi.CL * agric[i] + b.forest.psi.CL * forest[i] +
b.mosaic.psi.CL * mosaic[i] + b.grass.psi.CL * grass[i] +
b.psi.D.CL * z.D[i]
    }
    #-------------------------------------------------
    for (i in 1:n) {

     z.AC[i] ~ dbern(psi.AC[i])

    # Asian golden cat (affected by dhole and clouded leopard)
logit(psi.AC[i]) <- a.psi.AC + b.elev.psi.AC * elev[i] +
b.prey.psi.AC * AC.prey[i] + b.TC.psi.AC * TC[i] +
b.VillDens.psi.AC * villdens[i] + b.rough.psi.AC * rough[i] +
b.agric.psi.AC * agric[i] + b.forest.psi.AC * forest[i] +
b.mosaic.psi.AC * mosaic[i] +
b.grass.psi.AC * grass[i] + b.psi.D.AC * z.D[i] + b.psi.CL.AC
* z.CL[i]

                    }

#+++++++++++++++++++++++++++++++++++++++++++++++++++++++++++

    for (i in 1:n) {

    z.LC[i] ~ dbern(psi.LC[i])

    #++++++ Leopard cat (affected by Asian golden cat) ++++++

logit(psi.LC[i]) <- a.psi.LC + b.elev.psi.LC * elev[i] +
b.prey.psi.LC * LC.prey[i] + b.TC.psi.LC * TC[i] +
b.VillDens.psi.LC * villdens[i] + b.rough.psi.LC * rough[i] +
b.agric.psi.LC * agric[i] +
b.forest.psi.LC * forest[i] + b.mosaic.psi.LC * mosaic[i] +
b.grass.psi.LC * grass[i] + b.psi.AC.LC * z.AC[i]

    }

#+++++++++++++++++++++++++++++++++++++++++++++++++++++++++++

    for (i in 1:n) {

    z.MC[i] ~ dbern(psi.MC[i])

  # Marbled cat (affected by Asian golden cat and Leopard cat)
logit(psi.MC[i]) <- a.psi.MC + b.elev.psi.MC * elev[i] +
b.prey.psi.MC * MC.prey[i] + b.TC.psi.MC * TC[i] +
b.VillDens.psi.MC * villdens[i] + b.rough.psi.MC * rough[i] +
b.agric.psi.MC * agric[i] + b.forest.psi.MC * forest[i] +
```

```
b.mosaic.psi.MC * mosaic[i] + b.grass.psi.MC * grass[i] +
b.psi.AC.MC * z.AC[i] + b.psi.LC.MC * z.LC[i]

                    }
#+++++++++++++++++++++++++++++++++++++++++++++++++++++++++++

#---- DETECTION PROBABILITY

    for (i in 1:n) {
    for (j in 1:m) {

    y.D[i,j] ~ dbern(apparent.p.D[i,j])
    apparent.p.D[i,j] <- z.D[i] * p.D[i,j]

    #================= Dhole ============================

    logit(p.D[i,j]) <- a.p.D + b.prey.p.D * D.prey[i]

    #=========================================================
    }
    }

    for (i in 1:n) {
    for (j in 1:m) {

    y.CL[i,j] ~ dbern(apparent.p.CL[i,j])
    apparent.p.CL[i,j] <- z.CL[i] * p.CL[i,j]

    #========== Clouded leopard (affected by Dhole)======

logit(p.CL[i,j]) <- a.p.CL + b.prey.p.CL * CL.prey[i] +
b.p.D.CL * y.D[i,j]

    #=============================================================

    }
    }

    for (i in 1:n) {
    for (j in 1:m) {

    y.AC[i,j] ~ dbern(apparent.p.AC[i,j])
    apparent.p.AC[i,j] <- z.AC[i] * p.AC[i,j]

#===== Asian golden cat (affected by dhole and clouded
leopard) ==================================

logit(p.AC[i,j]) <- a.p.AC + b.prey.p.AC * AC.prey[i] +
b.p.D.AC * y.D[i,j] + b.p.CL.AC * y.CL[i,j]

    #=========================================================
```

```
    }
    }

    for (i in 1:n) {
    for (j in 1:m) {

    y.LC[i,j] ~ dbern(apparent.p.LC[i,j])
    apparent.p.LC[i,j] <- z.LC[i] * p.LC[i,j]

    #========== Leopard cat (affected by golden cat) =========

logit(p.LC[i,j]) <- a.p.LC + b.prey.p.LC * LC.prey[i] +
b.p.AC.LC * y.AC[i,j]

    #=========================================================
    }
    }

    for (i in 1:n) {
    for (j in 1:m) {

    y.MC[i,j] ~ dbern(apparent.p.MC[i,j])
    apparent.p.MC[i,j] <- z.MC[i] * p.MC[i,j]

    #=== Marbled cat (affected by golden cat and leopard cat)

logit(p.MC[i,j]) <- a.p.MC + b.prey.p.MC * MC.prey[i] +
b.p.AC.MC * y.AC[i,j] + b.p.LC.MC * y.LC[i,j]

#=========================================================
    }
    }
    }
```

Chapter 5

Conservation priority landscape for meso-felids and dhole in Lao PDR

In preparation for submission to *PLOS*

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Abstract

Conservation initiatives for medium-sized felids and dhole have been extremely limited by the lack of knowledge on ecology and distribution of the species in Lao PDR. Detailed knowledge about the geographic occurrence of a species is crucial for the development of effective conservation measures. This study aims to provide spatially predictive habitat suitability models of clouded leopard *Neofelis nebulosa*, Asian golden cat *Catopuma temminckii* and dhole *Cuon alpinus* to facilitate decision making for carnivore conservation in Lao PDR. Results from multi-species occupancy modelling based on camera trap data of 2015/2016 from the Nam Et - Phou Louey National Protected Area were used to further conduct predictive habitat suitability mapping. Our findings highlight importance of the National Protection Forest Areas for the conservation of carnivore species in the country, especially in northern provinces and along the central Annamite landscape. We propose a study approach that generates visual support and quantitative information that are useful for conservation planning. Besides, our proposed approach can be easily adjusted for the study of other species.

Key words: *Cuon alpinus*, habitat suitability, *Neofelis nebulosa*, *Pardofelis temminckii*, species distribution modelling, Lao PDR.

Introduction

Wildlife populations in Lao People's Democratic Republic (Lao PDR) are negatively impacted by overexploitation for both subsistence and trade, and subjected to increasing habitat loss (Johnson *et al.* (2003). While wildlife hunting and utilization are considered an integral part of rural livelihoods in the country, the lack of effective management plans for wildlife at the national level poses a challenge to the conservation of endangered species and species

biodiversity. When resources for species conservation are limited, careful and effective conservation planning is required. This involves prioritization of management areas and identification of the best possible ways to use limited resources in an efficient manner (Pressey and Bottrill 2009). To achieve this, detailed knowledge about the geographic occurrence of key species is required as part of a suite of tools to support the development of effective conservation measures (Kaschner *et al.* 2006).

Lao PDR is home to various globally important carnivore communities that are relatively rare and of conservation concern (Duckworth *et al.* 1999b; Johnson *et al.* 2006b; Johnson *et al.* 2009; Johnson 2012; Kamler *et al.* 2012; Coudrat *et al.* 2014; Johnson *et al.* 2016). The country harbours potentially important populations of the Endangered dhole *Cuon alpinus* (Kamler *et al.* 2012; Kamler *et al.* 2015), the Vulnerable clouded leopard *Neofelis nebulosa* (Grassman *et al.* 2016a) and the Near Threatened Asian golden cat *Catopuma tamminckii* (Johnson *et al.* 2009; McCarthy *et al.* 2015a). The dhole (10 - 20kg) is a carnivore that lives in packs (with often > 10 members) and a habitat generalist making use of various habitats from dense evergreen forest to open dry dipterocarp forest (Johnsingh 1985; Van Valkenburgh 1991; Duckworth *et al.* 1999b; Kamler *et al.* 2015). The species preferably preys upon medium-sized ungulates (40 – 60kg; Selvan *et al.* 2013a). The clouded leopard (11- 23kg), on the other hand, is highly arboreal and strongly associated with forest habitats, especially primary evergreen forest (Nowell and Jackson 1996; Sunquist and Sunquist 2002; Grassman *et al.* 2005a; Austin *et al.* 2007). The species preys upon small and medium sized ungulates as well as primates, porcupines, quarrels, and pheasants (Grassman *et al.* 2005a). Similar to the clouded leopard, the Asian golden cat (9 – 16kg) is often associated with closed forest habitats and its diet consists of muntjacs, squirrels and small rodents (Nowell and Jackson 1996; Grassman *et al.* 2005a; McCarthy *et al.* 2015a; McCarthy *et al.* 2015b). Since tiger *Panthera tigris* and leopard *Panthera pardus* seemed to have become extirpated from Lao PDR (Rostro-García *et al.* 2016), the above mentioned three medium-sized carnivores are the remaining top predators in Lao

PDR. Globally, their populations are declining and are severely fragmented due to hunting, habitat loss and prey depletion (Kamler *et al.* 2015; McCarthy *et al.* 2015a; Grassman *et al.* 2016a). This makes their conservation of paramount significance. Despite their importance, they have received little conservation attention, and little has been done to investigate their distribution across the landscapes of Lao PDR.

As geographical information system (GIS) approaches and computational power have become more advanced in recent years, habitat suitability models have been developed and widely used for quantitatively predicting distributions of terrestrial species (Peterson and Navarro-Sigüenza 1999; Peterson 2001; Zaniewski *et al.* 2002; Store and Jokimäki 2003; Hearn *et al.* 2018b). Specifically, habitat suitability models can quantify the habitat suitability allowing comparison of areas and species. Besides, with visually mapped outputs, understanding of species habitat distribution across landscapes can be enhanced. Such outputs can be used to direct interventions for the protection of specific areas to ensure species survival (Sanderson *et al.* 2002; Johnson *et al.* 2006a). These types of models can also be used to further predict where species may move to in case new threats emerge or are impacted by habitat lost (Guisan and Thuiller 2005).

This study aims to provide spatially predictive habitat suitability models of the above mentioned three medium-sized carnivores to facilitate decision making for carnivore conservation in Lao PDR. Given the extent of their habitat requirements, we believe that successful conservation of these species will greatly benefit the conservation of smaller carnivores and their prey. Specifically, in this study, we quantified the habitat according to its suitability for the three considered species and we produced predictive maps highlighting areas of high conservation importance thereby providing recommendations that may help guide conservation planning of the target species. We predicted that majority of the highly suitable areas for all three species will be located within the borders of NPAs. This is due to the fact that the protected areas system in Lao PDR was created on the basis that NPAs contain various important habitats that support

the maintenance and protection of biological diversity. Furthermore, given their protected status, anthropogenic disturbances are likely to be lower in NPAs.

Materials and Methods

Study area

Lao PDR is a landlocked, developing country in Southeast Asia, sharing its borders with China, Vietnam, Cambodia, Thailand and Myanmar (Fig.1). Topographically, mountainous areas with steep slopes and rugged terrain dominate the northern part and along the eastern border with Vietnam, while the southwestern part along the Mekong river is defined by lowland alluvial plains (Hett *et al.* 2011). Overall the landscape is marked by near-natural vegetation and smallholder agricultural systems, which results in a mosaic landscape of different degrees of agricultural use intensity (Messerli *et al.* 2011). Forests are a dominant landscape feature in Lao PDR and livelihoods of many local people depend on forest resources (Rigg 2006). There are currently 24 NPAs and 49 National Protection Forest Areas (NPFA) (Fig.1), covering 15% and 36% of Lao PDR's landscape respectively (Sophathilath 2010).

For this study, we used camera trap data from the 2015/2016 survey in the Nam Et – Phou Louey National Protected Area (NEPL), the second largest NPA in Lao PDR (5,969 km^2 with rugged topography) and located in the northeast part of the country (Fig.1). Its elevation ranges from 400 - 2257 m, of which >60% is above 1000 m and 91% with slopes >12% (Johnson 2012). Vegetation is largely dominated by dry evergreen and semi-evergreen forests. However, around one third of the park is degraded forest with a canopy cover of less than 20%.

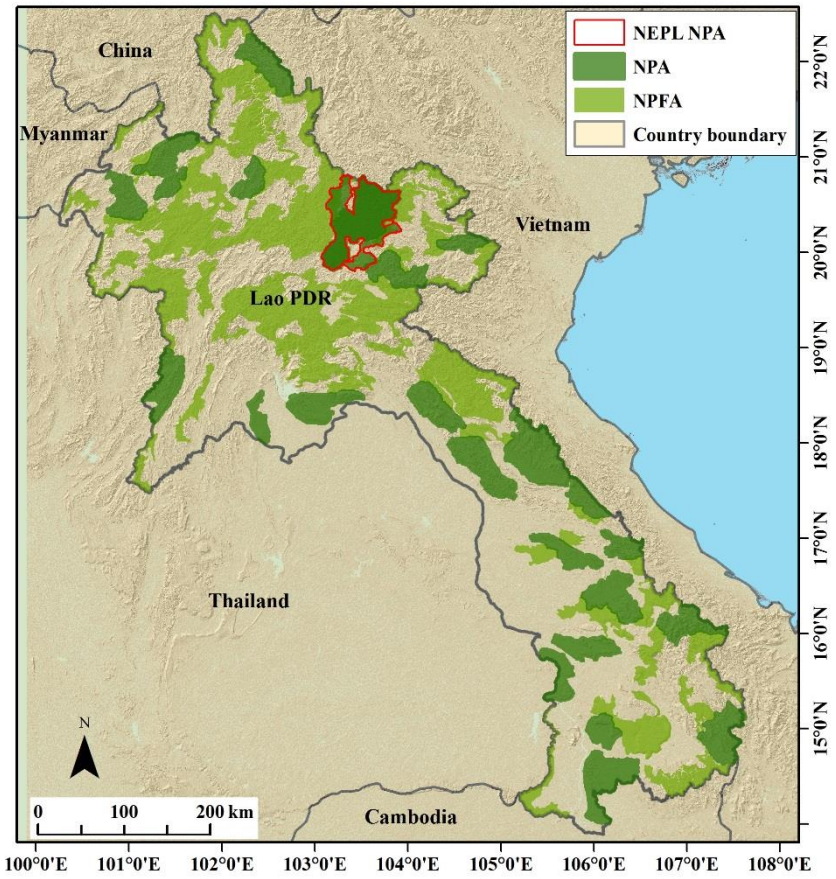


Fig. 2: Map of Lao PDR showing the location of Nam Et - Phou Louey National Protected Area (NEPL, all national protected areas (NPA) and national protected forest areas (NPFA)

Data collection

The camera trap survey started in March 2015 and was carried out in three ~200km^2 blocks over three periods. There were 80 camera stations set at 1-1.5km in each block. We used a mixture of infrared camera trap models: CuddeBack Ambush IR (infrared) – Model 1187 camera traps by CuddeBack Digital, RECONYX HYPERFIRE HC500, and MAGINON – WK 3 HD by Supra Foto-Elektronik-Vertriebs-GmbH.

The camera trap stations were located between 629- 2185m in altitude (Table 1) with 16% of the stations below 1000m, 16% between 1000 to 1500m, and 68% above 1500m. About 63% of the sites were in areas of closed forest, evergreen and high density semi-evergreen forests.

The camera traps were placed mostly along ridge lines and animal trails, and at points where trails meet streams. Each camera was mounted onto a tree trunk and ensured that its motion beam was set at 35cm above the centre of the trail (approx. shoulder height of medium size felid, especially clouded leopards). Each survey period lasted for a minimum of 50 days (Table 1).

Table 1: Camera trap survey dates, effort and altitude in four blocks in Nam Et - Phou Louey National Protected Area, Lao PDR, during 2015 - 2016

Block, site name	Date	Duration (days)	Stations (cameras)	Trap nights	Altitude (m)
1, Nam Poung - Na Vaen	Mar - May. 2015	52	80 (158)	3200	983 - 2185
2, Pha Daeng	May - Jul. 2015	51	80 (156)	3282	709 - 1739
3, Phoupha - Siphou	Feb - Apr. 2016	50	80 (160)	3003	629 - 1514

Data analysis

Data analysis consisted of two phases – species occupancy modelling (which was performed as part of the analysis for Chapter 5) and predictive habitat suitability mapping. The results related to habitat factors from the occupancy modelling were integrated into producing the species habitat suitability model.

Occupancy modelling

We adopted a Bayesian multi-species occupancy modelling framework following the approach by Waddle *et al.* (2010). This approach was used to test for spatial associations between species and evaluate the effect of site covariates on occupancy. Details on model compilation and assumptions are outlined in the Methods section of Chapter 5. In order to investigate species habitat suitability factors, we considered a number of variables. Based on previous studies (Jenks *et al.* 2012; Srivathsa *et al.* 2014; Hearn *et al.* 2016a; Hearn *et al.* 2016b; Hearn *et al.* 2016c; Mohamed *et al.* 2016; Hearn *et al.* 2018a; Hearn *et al.* 2018b; Macdonald *et al.* submitted) covariates that we considered for modelling occupancy included elevation, surface roughness or ruggedness (to account for topographic heterogeneity), percent forest cover, settlement/village density, and four land cover categories (Table 2). To account for fine-scale heterogeneity of the landscape, we resampled all our covariate raster layers to 90m grid size resolution. The elevation layer used in this study was from the 30m Shuttle Radar Topography Mission (Jarvis *et al.* 2008). Roughness was derived from the digital elevation layer using the Geomorphometry & Gradient Metrics Toolbox (Evans *et al.* 2014) in ArcGIS 10.2.2 (Environmental Systems Research Incorporated, ESRI, Redlands, CA, USA, 2011). Percent forest cover was obtained from Hansen *et al.* (2013). The settlement/village density was calculated using the Kernel Density tool in ArcGIS (using 20 km search radius). The land cover categories were derived from the global land cover 2015 layer provided by the European Space Agency (ESA) that was refined with a NEPL NPA land cover layer from 2015. For this study we reclassified the global land cover map into four categories including agriculture, forest, grassland and mosaic (regenerating vegetation). For all continuous variables, we calculated focal mean using the circular window method with 8000m radius. The radius of focal mean was selected based on other studies on medium to large size felids showing selection for broad scales (Hearn *et al.* 2018a; Macdonald *et al.* submitted). For each land cover category, we calculated in ArcGIS the percentage of the landscape (PLAND) occupied by each land cover type using

8000m moving window. We also included prey encounter rate (PER), which was the number of independent events (>1 hour interval) per 100 trap days (Carbone *et al.* 2001). For each carnivore, a separate PER was calculated based on their known prey species and was considered for both occupancy and detection modelling.

Table 2: Habitat covariates, metrics calculated, and data sources. Focal mean was calculated for all continuous variables. PLAND (percentage of landscape) was calculated for categorical variables.

Covariate	Metric	Data source
Elevation	Focal mean & SD	Jarvis *et al.* 2008 (http://srtm.csi.cgiar.org)
% Forest cover	Focal mean & SD	Hansen *et al.* 2013 (http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.2.html)
Settlement density	Focal mean & SD	Lao National Geographic Department
Roughness	Focal mean & SD	Evans *et al.* 2014 (ArcGIS Geomorphometry & Gradient Metrics Toolbox; http://evansmurphy.wixsite.com/evansspatial/arcgis-gradient-metrics-toolbox)
Land cover classes: agricultural, forest, grassland and mosaic	PLAND	ESA CCI Land Cover layer 300m 2015 (www.esa-landcover-cci.org/?q=node/175); Nam Et - Phou Louey National Protected Area land cover layer 30m 2015 by the Wildlife Conservation Society Lao PDR.

Prior to performing occupancy modelling in the Bayesian framework, collinearity of continuous site covariates was assessed by pairwise correlation using Spearman's rank correlation coefficients (Dormann *et al.* 2013). Any combination of covariates that have a pairwise correlation > 0.7 was considered correlated and the most informative covariates were retained for final modelling processing. Selection of the covariates for each species was done by testing for the most informative variables using single-species, single-season habitat use models in the R package "unmarked" version 0.12-2 (Fiske and Chandler 2011) in R 3.4.3 (R Core Team 2017) following a two-step process as described by Long *et al.*(2011). Once habitat covariates for each species were selected, they were integrated into a Bayesian framework to estimate their effects. Detection history for each species was compiled separately where a 0 and a 1 denote non-detection and detection, respectively, in a survey period/site. Data from five trap days at the site were aggregated as a single survey occasion, following Johnson *et al*. (2009). Overall, there were 10 sampling occasions.

Following the similar situation as the study by Bischof *et al.* (2014) where our data were inadequate for precise estimates of some parameters associated with occupancy interaction effects, we decided to use relatively narrow priors with a normal distribution (mean = 0, precision = 0.1) for all species occupancy interaction effects and compared the extent and direction of the posterior distribution's deviation from 0 to assess the level of support for avoidance or association. We used uninformative priors with a uniform distribution defined on the log-odds [-10, 10] for other parameters. We fitted the Bayesian model in JAGS (Plummer 2003) via R platform (R Core Team 2017). The Makov Chain Monte Carlo (MCMC) algorithm was run for 600,000 iterations for 3 chains with the thinning rate of 50 and discarding the first 100,000 samples. We assessed convergence using the Gelman-Rubin statistic where value <1.1 denotes convergence (Gelman and Rubin 1992).

Predictive habitat suitability modelling

Under this analysis process a series of steps were undertaken. First, we produced habitat suitability maps for each species separately based on the posterior mean of beta coefficients of habitat covariates that contributed to the prediction of species occupancy. We used the arbitrary threshold of ***f*** value >60% related to the posterior mean to select variables that were then used for mapping species habitat suitability. The value of ***f*** represents the confidence that a parameter is positive or negative when 0 falls in the parameter's 95% credible interval. Only variables with available GIS layers were selected. As such, we fully acknowledged that the higher level of accuracy in the map outputs were compromised. However, by integrating the outputs of the occupancy modelling, we accounted for imperfect detection. A similar approach was also used in the clouded leopard study in Malaysia by Tan *et al.* (2017). To get probability of species occurrence *psi*, we used the following transformation $psi = exp(z) / (1 + exp(z))$, where *z* is the linear combination of coefficients multiplied by the independent variables. Second, to measure for the strength of the linear relationship among the three different species habitat suitability map layers, we calculated Pearson's correlation and hereafter calculated mean absolute difference (MAD) to assess for variation between them. Third, we generated three maps of pairwise comparison of their habitat suitability distribution where areas that are more suitable for one species (compared to another) are highlighted. Fourth, we generated a carnivore habitat suitability landscape map to highlight areas where high conservation impact can be delivered to important carnivore communities. Under this step, we used *psi* of ≥ 0.7 as a threshold to identify/classify highly suitable areas for each species and thereafter we overlaid all three classified layers to define areas where all three species, only two, and only one species occur. Furthermore, we determined the percentage of each area category that are under protection (i.e., fall within NPAs or NPFAs) upon which we could base further management and conservation recommendations.

Since the predictive mapping process was done using data set from solely one protected area for the whole country, it is importance to carry out ground-truthing to validate the predictive results. Due to time constraints, this validation process was not performed. Reconnaissance camera trap surveys and data on the species in questions recorded from other parts of Laos could be used to validate our findings. These will be carried out in the near future prior to the implementation of the modelling outputs.

Results

Originally, the occupancy analysis was carried out for five carnivore species which included the leopard cat *Prionailurus bengalensis* and marbled cat *Pardofelis marmorata* in addition to the target species for this study. The results related to the occupancy of dhole, clouded leopard and Asian golden cat are reported in Table 3. We found that dhole occurrence had a strong positive association with density of settlement areas while exhibiting a strong negative association with mosaic areas. Although not very strong, the results also showed a positive association with elevation for dhole. For clouded leopard, since none of the habitat factors proved to be highly significant, we selected those factors which had a greater than 60% certainty that the parameter had a positive or negative association (Table 3) for the habitat suitability mapping. These include: roughness, percent tree cover, and percent of grassland cover. For the Asian golden cat, there was slight evidence suggesting its association to areas with high tree cover and grasslands. In conjunction with these two factors, we also included the density of settlements that showed a positive effect on the species occurrence, based on the same 60% level of confidence threshold.

Table 3: Estimates of standardized regression coefficients ± standard deviation of factors affecting occupancy and detectability for clouded leopard, Asian golden cat and dhole, based on the 2016 camera trap survey data in Nam Et - Phou Louey National Protected Area. Estimates are given on the logit scale with stars indicating significant effects on species occupancy estimation. Significance was assessed using an approximation of the Wald statistic, defined as the coefficient divided by its standard error.

	D	**CL**	**AC**
Habitat factors for *psi()*	*C. alpinus*	*N. nebulosa*	*C. temminckii*
Intercept	6.24 ± 2.36	1.61 ± 3.53	0.24 ± 4.19
Elevation	1.15 ± 2.18*		
Prey encounter rate	-2.25 ± 1.97		
% Tree cover		1.49 ± 3.85 *	5.66 ± 3.17* *
Roughness		2.48 ± 2.84 *	
Settlement density	6.99 ± 2.39***		1.49 ± 2.38 *
% Agriculture			
% Forest			
% Mosaic	-5.77 ± 2.32***		0.17 ± 2.22
% Grassland		1.50 ± 4.29 *	6.47 ± 2.94**
D presence		5.64 ± 3.08* *	-1.17 ± 5.00
CL presence			6.57 ± 3.59
AC presence			
LC Presence			

**** represents strong evidence as the credible interval of the posterior mean does not include zero, ** represents slight evidence, and * represents greater than 60% confidence that a parameter is positive or negative.*

The predictive habitat suitability maps showed similarities in the predicted probability of occurrence between the clouded leopard and Asian golden cat. The suitable habitat mainly concentrated in the northern part of the country and stretched along the eastern boundary of the landscape. For both species, the suitable habitats were mostly in continuous and large patches. For the dhole, the suitable habitat distributed evenly across the landscape and there were more potential habitat patches along the southwest of the country's boundary compared to that of the other two species. Although most patches for dhole seemed to have some small linkages among them, there were also a lot of fragmented, smaller patches. The NEPL, the area in which the study was conducted, turned out to be an area with low suitability for all three species.

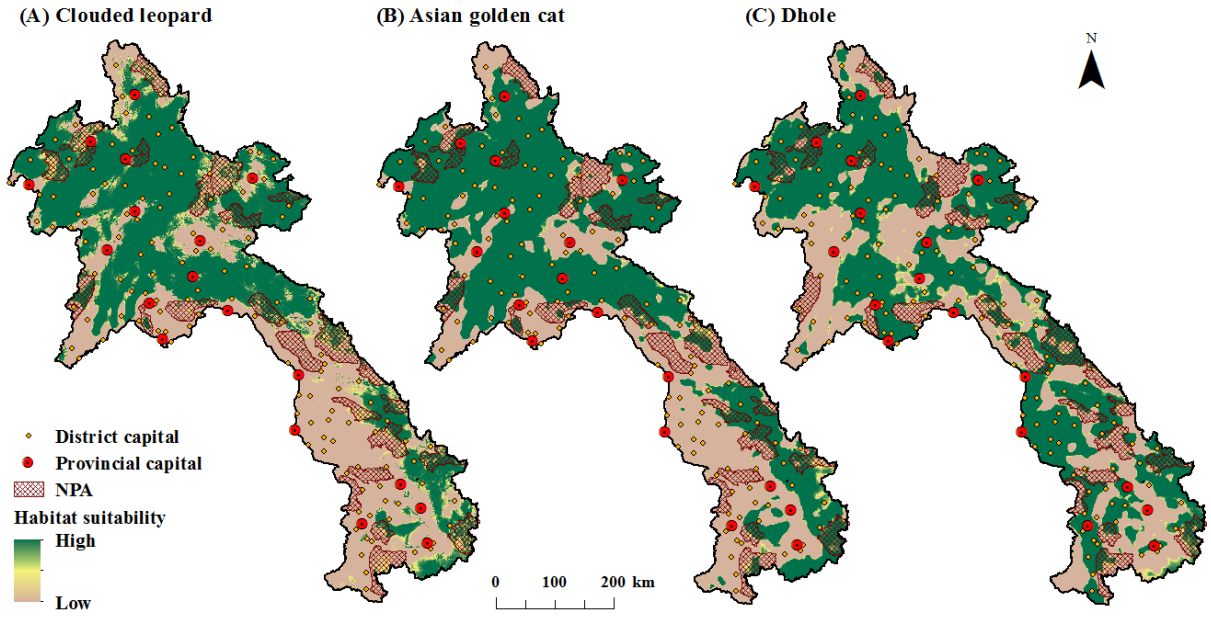


Fig. 3: Maps showing species predicted occurrence in Lao PDR for (A) Clouded leopard *Neofelis nebulosi*, (B) Asian golden cat *Catopuma temminckii* and (C) Dhole *Cuon alpinus*.

The results of the habitat correlation and mean absolute difference (MAD) investigation (Table 4) further suggested that habitat of the Asian golden cat was strongly associated with that of the clouded leopard (correlation = 0.862 and MAD = 0.082). We found that occurrence of both the clouded leopard and Asian golden cat were moderately associated with that of the dhole. There was no clear evidence that the association of occurrence between clouded leopard and dhole was stronger than that between Asian golden cat and dhole.

Table 4: Relationship between occurrence probability map predictions for three medium-sized carnivores.

			MAD	
		Clouded leopard	**Asian golden cat**	**Dhole**
Correlation	**Clouded leopard**	x	0.082	0.247
	Asian golden cat	0.862	x	0.231
	Dhole	0.414	0.441	x

Values in yellow are Pearson's correlation between probabilities of occurrence across the country. Values in blue are the mean absolute difference (MAD) in probability of occurrence across the country.

The pairwise habitat comparison maps (Fig.3) highlight areas that are more suitable for one species versus another. The habitats of the clouded leopard and Asian golden cat spatially overlapped, and the strength of habitat suitability was spatially similar for both species (Fig.3.A). The patches that were more suitable for clouded leopard (green areas) were mainly

distributed in the northeast of the country, while areas that were more suitable for the Asian golden cat (in red) were quite small, fragmented and distributed evenly from north to south across the country. There was spatial and quantitative difference in habitat suitability for clouded leopard and dhole and dhole and Asian golden cat, where areas along western boundary and central part of the country (in red for Fig.3.B and in green for Fig.3.C) being more suitable for dhole whereas the areas distributed in the northern part and along eastern boundary were more suitable for the clouded leopard and Asian golden cat. The areas predicted to be more suitable for dhole correlates with densely populated zones whereas for the clouded leopard and Asian golden cat, these correlate with the more mountainous areas.

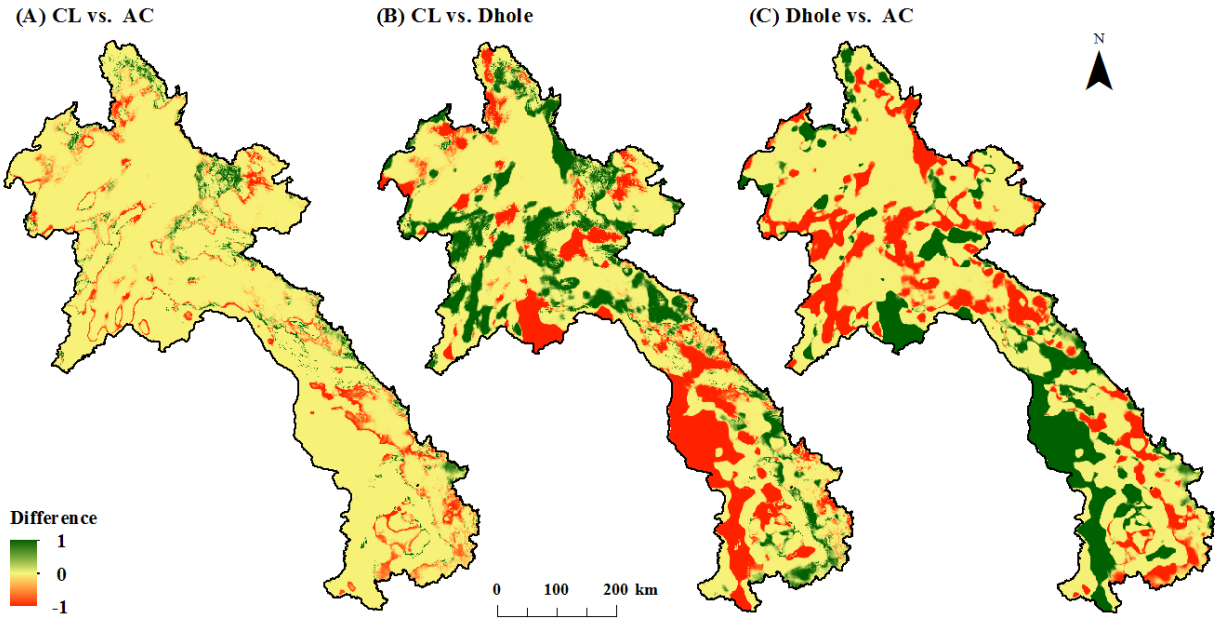
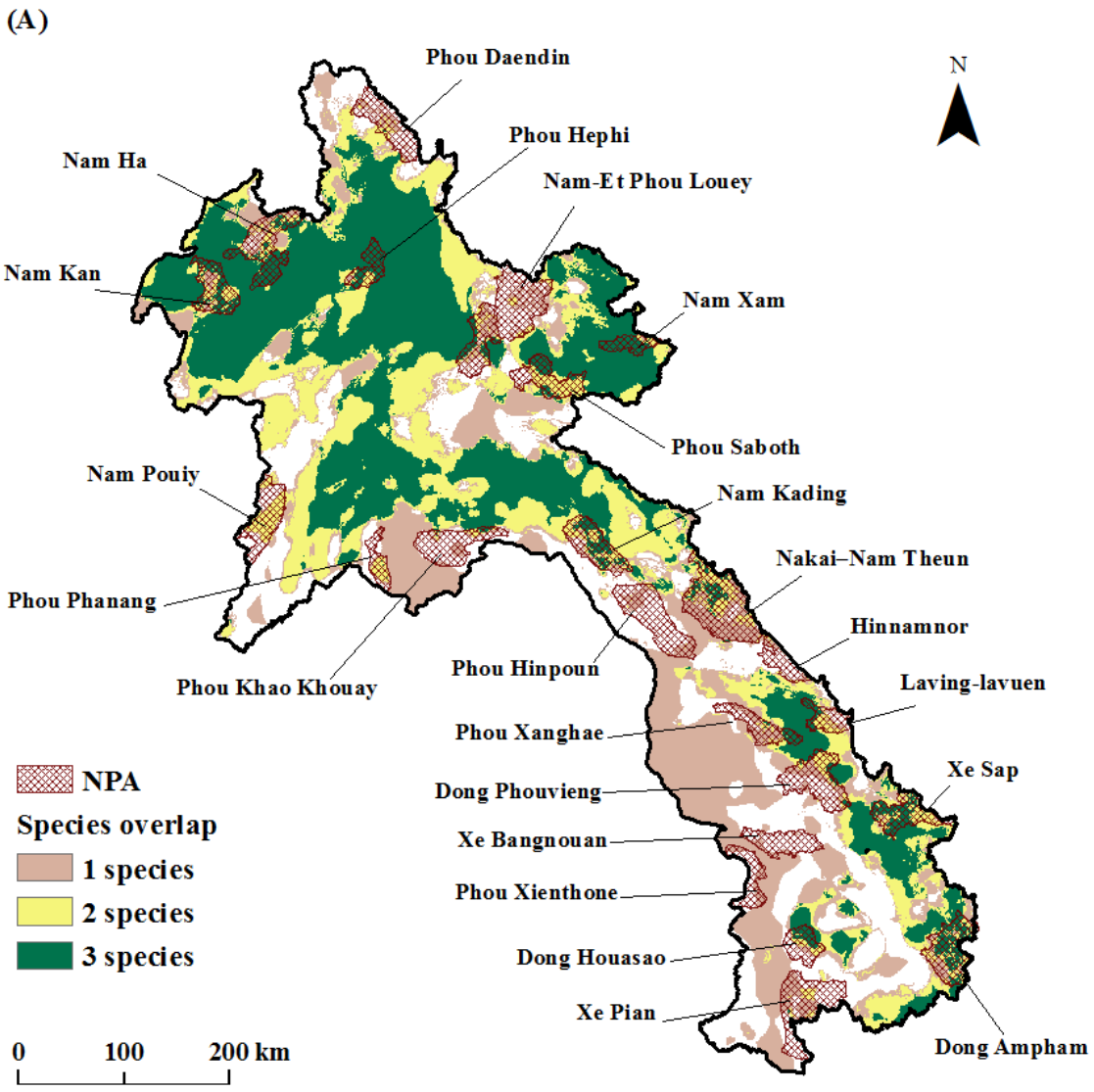


Fig. 4: Maps showing areas of difference between predicted occurrences of pairwise species. Map (A) shows the difference between the clouded leopard (CL) and Asian golden cat (AC). Map (B) shows the difference between the clouded leopard and dhole. Map (C) shows the difference between the dhole and Asian golden cat.

The carnivore habitat suitability map output (Fig. 4) highlighted three categories of areas: suitable for only one species, two species, and all three species. It showed the majority of the

northern area of the country being suitable for three species with smaller pockets distributed in the south-eastern, mountainous part of the country. This area covers 32% of the whole country whereas area suitable for one species and two species covered 23% and 22% of Laos, respectively. The map showed that most of the suitable habitat for three species were outside of NPAs (Fig.4.A). Surprisingly, neither of the top two largest NPAs in Lao PDR (NEPL and Nakai - Nam Theun) appear to contain large areas for all three species. The NPFAs, on the other hand, seem to cover much more of the suitable habitat for at least two species, compared to the NPAs (Fig.4.B), especially highly suitable areas for all three species located in the north of the country. Out of the three habitat suitability categories, the suitable area for one species was the category that the NPAs covered the most (Table 5). The NPFAs covered about 43.5%, 43% and 35% of the suitable area for three, two and one species, respectively (Table 5). It is important to note that the NPFAs covered more of all area categories also because they cover an area over 2.5 times larger than the total NPAs.


(A)
Phou Daendin
Phou Hephi
Nam Ha
Nam-Et Phou Louey
Nam Kan
Nam Xam
Phou Saboth
Nam Pouiy
Nam Kading
Nakai–Nam Theun
Phou Phanang
Hinnamnor
Phou Hinpoun
Laving-lavuen
Phou Khao Khouay
Phou Xanghae
Xe Sap
Dong Phouvieng
Xe Bangnouan
Phou Xienthone
Dong Houasao
Xe Pian
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Species overlap
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2 species
3 species
0
100
200 km

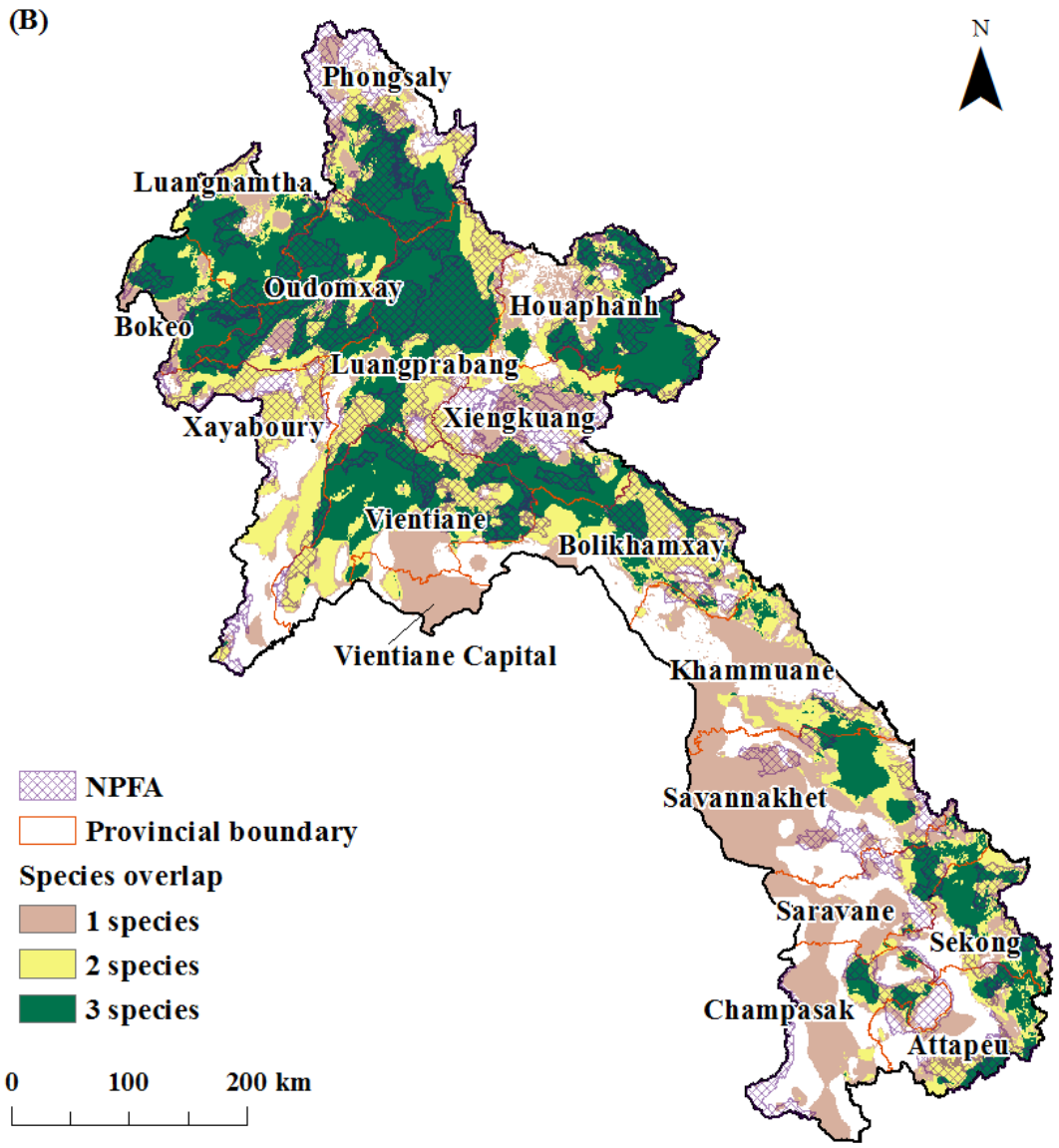


Fig. 5: A map showing overlapping areas of predicted occurrence of three carnivore species: clouded leopard, dhole and Asian golden cat with: (A) an overlay of the National Protected Areas (NPA) and (B) an overlay of the National Protection Forest Areas (NPFA).

Table 5: Percentage of predicted species occurrences under national protected areas (NPA) and national protection forest areas (NPFA)

	All 3 species (CL, AC, Dhole)	2 species	1 species
NPA	10.271	12.641	14.424
NPFA	43.475	43.077	35.236

Discussion

This study is the first attempt to predict the habitat distribution of medium-sized carnivores (i.e., the remaining top-predators after the extirpation of wild tigers and leopards) at the national level in Lao PDR. While we are aware that our inference may be seen as an overgeneralisation of the real situation based on a small data set from the Nam Et - Phou Louey National Protected Area (NEPL) alone, it was the best data set available from one of the most intensive camera trap studies ever conducted in the country (Johnson *et al.* 2009; Coudrat *et al.* 2014). Although our model results showed the probability of the clouded leopard, Asian golden cat and dhole to be quite low, we believe that the NEPL potentially still harbours the largest populations of these three species compared to elsewhere in the country (Coudrat *et al.* 2014; Kamler *et al.* 2015). We therefore believe that the NPA is the most appropriate place to on which to base our habitat suitability investigation of these species.

The result of the habitat suitability model for the clouded leopard slightly contradicted our original hypothesis that the NEPL would contain a large continuous patch of the most suitable habitats for the species, based on the higher number of records of clouded leopard in NEPL

than other protected areas where similar intensive camera trap surveys were previously conducted, such as Nakai - Nam Theun (Coudrat *et al.* 2014) and Nam Kading (unpublished data). The suitable habitat instead distributed heavily around the edges of the NPA with some small patches inside the NPA (Fig.2.A). This could be due to the fact that the variables included for this species habitat model did not originally provide a strong explanatory power for occurrence of the clouded leopard in our occupancy modelling. Using the estimated coefficient values (with such large uncertainty) of these variables could have therefore resulted in such unexpected results. However, the results showed that a number of NPAs in the north and along the eastern boundary of the country contain suitable habitat for the species which is consistent with the previous report of species presence by Duckworth *et al.* (1999b), especially in Nam Ha, Nam Phouiy, Nam Xam, Phou Xanghe, Nam Kading, Nakai - Nam Theun, Dong Ampham, Dong Houasao and Xe Pien. From the overall habitat distribution of this species, most provinces in the north showed to be an important landscape for the species' conservation.

Based on the results of the habitat suitability, the NEPL is even less suitable for the Asian golden cat. Based on the suggestion that the species is a habitat generalist (Dhendup 2016), the variables that we included in the habitat suitability modelling (especially the % forest cover and % grassland cover) were believed to be reasonable. However, we found it hard to explain why the NEPL did not represent a suitable habitat for the Asian golden cat, apart from questioning the inclusion of the human settlement density factor (which originally did not provide a strong explanatory power to our occupancy model). Due to time constraints, we were unable to test how different the model would be if we excluded the human settlement density factor. This warrants future investigation. Compared to the habitat distribution models of the two other species, the model for the Asian golden cat showed more intact habitat patches. Similar to the habitat distribution of the clouded leopard, that of the Asian golden cat occupied more NPAs (15 out of 24 NPAs) from north to south. The majority of these NPAs were reported to contain the species (Duckworth *et al.* 1999b), these include: Nam ha, Nam Phouiy, Nam

Xam, Phou Xanghe, Nam Kading, Nakai - Nam Thuen, Dong Ampham, Dong Houasao and Xepien. We also showed that a large chunk of suitable habitat is outside of the NPAs and covers the majority of the northern landscape, which again suggests the importance of the northern provinces for the species' conservation.

The predicted habitat distribution of dhole highlighted some unexpected areas, especially those large provincial capitals along the western portion of the country (Fig.2.C). While attraction to settlement areas can be explained by dhole's livestock predation (Duckworth *et al.* 1999b; Thinley *et al.* 2011; Hayward *et al.* 2014; Aryal *et al.* 2015), the indication that urban areas are suitable for the species should be considered with caution. Our sampling design did not include large urban areas, rather only for small settlements, so we could not really test for the effect of large urban areas. We believe that the attraction to human settlement is more relevant in areas near to NPAs due to villages being located in and around these areas, especially the NEPL, in which local populations graze their livestock (Johnson 2012). In the densely populated and highly disturbed areas, the risk to their populations is too high, which makes dhole occurrence to be even more unlikely in such areas. However, more than 10 NPAs from north to south showed to contain dhole's suitable habitat which is also consistent with a previous study (Duckworth *et al.* 1999b). According to Duckworth *et al.* (1999b), dhole population is widespread but at low densities and reported to exist in many of the NPAs across Lao PDR, including: NEPL, Nam Xam, Nam Ha, Nam Kading, Nakai - Nam Theun, Xe Sap, Dong Ampam, Xe Pien, Dong Houa Sao, and Phou Xamghe.

Our habitat correlation and difference analysis highlight strong association between the clouded leopard and the Asian golden cat habitats which confirms our findings in Chapter 5 showing a slight evidence of positive association between the species. The strong habitat association between these two species means habitat conservation of one could benefit the other. Based on the species interaction analysis results in Chapter 5, we expected the habitat association between dhole and clouded leopard to be higher than between dhole and Asian golden cat. Our results

of the two pairwise assessment (clouded leopard against dhole, and dhole against Asian golden cat), however, did not support this assumption. Instead, both clouded leopard and Asian golden cat showed a moderate and practically equal level of habitat association with dhole (Table 4). Despite the lower habitat overlap of all three species compared to the overlap between the clouded leopard and the Asian golden cat, the predicted level of habitat association/overlap (of about 40%) for all three species suggests optimal areas could still be identified to benefit the conservation of all three species.

Our main prediction that the majority of NPAs would represent suitable habitat for the three carnivores was not strongly supported by the findings from the habitat overlap analysis. While previous studies have suggested, in particular for clouded leopard and Asian golden cat, that occurrence is typically positively associated with closed forest habitats and intolerance to anthropogenic features (Duckworth *et al.* 1999b; Grassman *et al.* 2005a; McCarthy *et al.* 2015a; Grassman *et al.* 2016a), our habitat suitability mapping indicates that the suitable habitat for all three, as well as for at least two species, appeared to concentrate outside of NPAs (Fig.4.A) and more likely to fall within the NPFAs (Fig.4.B and Table 5). This would suggest the importance of conservation beyond just NPAs for these species, especially the landscapes in northern Lao PDR and along the Annamite mountain range in south-eastern Lao PDR. In doing so, this could create crucial linkages between important populations of medium-sized carnivores across both the northern and south-eastern landscapes.

The above finding, however, does not negate the importance of ongoing protection of NPAs for carnivore conservation. More than half of the NPAs in Lao PDR are under some form of multi-year financial and technical support as well as intermittent support to management (Robichaud *et al.* 2001; Fujita 2004). The NPAs that are most actively managed and that receive comprehensive, long-term management support include: Nam Phouiy, Nam Kan, Nam Ha, NEPL, Phou Khao Khouay, Nam Kading, Phou Hinpoun and Nakai - Nam Theun. Although the suitable habitat for all three species appears mismatched with these areas at a meta level,

there does remain some suitable habitat patches within these NPAs and the active management of these areas means these patches retain an important function as refuges (where threats to habitat loss occur at lower rates than non-protected areas) for our key species.

Our study could be verified and improved via a number of ways. First, multi-scale habitat suitability analysis should be considered because spatial niche segregation can happen at different scales (Hearn *et al.* 2018b). Second, prey species distribution should be mapped and integrated into the carnivore habitat suitability models. With this integration, not only the association between predator and prey can be inferred, but important prey-hotspots can also be identified. Third, since our analysis is based on a data set from a single NPA and the results could be biased towards characteristics of one area, integrating more data sets from other studies across the country could raise the accuracy of our prediction. Fourth, distance forest edge and rivers should be included in the model to test for their influence on species occurrence. Fifth, with regards to the human settlement bias (e.g., in the case of dhole suitable habitat distribution), the human settlement component should be limited to only certain remote and small villages, rather than all human settlements across the country. In this way, we can (at least partially) minimise the issue of dhole being associated with big urban areas whilst still modelling their likelihood to associate with livestock raising areas.

This is the first study to estimate suitable habitat distribution of top-carnivore species conducted for the whole Lao PDR. The study results provide useful information that can form the basis to guide conservation planning of the target species. Our methodological approach can easily be adjusted for other carnivore species. With this part of analysis completed, further study can be carried out looking at landscape connectivity, defining core habitat areas and important corridors linking these core areas for the maintenance of species populations. Knowing the locations of core areas and their linkages can help to raise their profile for carnivore conservation.

Acknowledgements

We thank the Wildlife Conservation Society, Laos, for their and the Nam Et - Phou Louey National Protected Area for their extensive in-kind support and for their efforts towards planning and implementing the research. For data collection and management, we thank Mr. Phonesouk Chanthalavong for his excellent assistance in field work preparation and implementation, and data management. We further thank Dr Zaneta Kaszta, Jan F. Kamler and Mr. Colin Moore for their guidance. The research was supported by a grant to DWM from the Robertson Foundation and National Geographic Society, for which we are deeply grateful.

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Chapter 6: General Discussion

Introduction

The aim of this thesis was to investigate interactions of sympatric hypercarnivores (felids and dholes). My study was motivated by two reasons. First, various studies have shown how important carnivores are in regulating an ecosystem (Terborgh *et al.* 2001; Sinclair *et al.* 2003; Smith *et al.* 2003; Steneck 2005; Ripple and Beschta 2006; 2007; Estes *et al.* 2011), yet many are experiencing a dramatic decline due to human-induced disturbances that negatively cause either direct or indirect impacts on their populations (Ripple *et al.* 2014; Rosenblatt *et al.* 2014; Gray *et al.* 2017a). Second, apart from the top predators (e.g., tiger *Panthera tigris* and leopard *Panthera pardus*), other hypercarnivores are poorly studied not only within Laos but across their range in SE Asia. I believe that the lack of understanding of their ecology poses a limitation to the management and conservation of their populations. Therefore, I seek to ask four questions related to: (i) status of all carnivores and prey species of Nam Et - PhouLouey National Protected Area (hereafter NEPL), to understand community structure and dynamics, (ii) overall densities and density trends of meso and small carnivores, to understand what is likely to happen when top predators (i.e. tigers) disappear from the system, (iii) spatial and temporal niche segregation, to understand factors facilitating coexistence of all sympatric mesocarnivores, and (iv) the distribution of suitable habitat across the country, to seek and promote their conservation beyond the NEPL.

I addressed each of the aforementioned research questions with the use of camera trap data. Species population data are not easy to obtain due to the various challenges regarding the ecology and habit of the target species for this study. Low detection probability is usually the case for surveying low density, nocturnal, solitary or shy species (McCarthy *et al.* 2008; Balme *et al.* 2009). Nevertheless, camera trap surveys have proved to be a useful method to monitor rare and/or cryptic animals (Karanth and Nichols 1998; O'Brien *et al.* 2003; Kays *et al.* 2011). This method is widely used and is considered to be one of the most robust, non-invasive and effective techniques for obtaining population level data on the abundance, distribution and

interactions of large mammalian carnivores (Ridout and Linkie 2009b; Ngoprasert *et al.* 2012; Wilting *et al.* 2012; Bernard *et al.* 2013; Lynam *et al.* 2013; Ross *et al.* 2013). Camera trap photographs, allow for the identification of uniquely marked individuals and thus facilitates the estimation of species densities through spatially explicit capture-recapture (SECR) (Karanth and Nichols 1998; Sollmann *et al.* 2014b), which was adopted in Chapter 3, whilst also yielding a wide variety of additional information for biologists (Trolliet *et al.* 2014). Camera trapping can produce presence-absence and distribution data for many species which can be further analysed (in Chapter 2 and Chapter 4) to investigate habitat preference, distribution drivers, and responses to disturbance (Gaston and He 2011; Rovero *et al.* 2014; Dénes *et al.* 2015). Temporal information can also be obtained from camera trap photographs, which allows for the study of species' activity patterns (Lynam *et al.* 2013; Ross *et al.* 2013) as was done as part of Chapter 4. While I understood that a dietary study would help to give a more complete picture of the species' interactions, I encountered a challenge of not collecting enough scat samples for the target species, specifically the clouded leopard and marbled cat, which could be due to their arborealism. Hence, the species diet could only be inferred from available literature. My research nonetheless yielded interesting findings.

Key Findings

Status of carnivores and their prey in NEPL

This study documented and confirmed the local extinction of leopard *Panthera pardus* as my survey failed to detect this species, and the last confirmed photograph from the site was in 2004 (Johnson *et al*. 2006). My study also documented the probable extirpation of tiger *P. tigris* as only two individuals were detected during the initial year of the survey. These two tigers were the same two individuals, and only individuals, photographed in NEPL in 2012 (Johnson *et al.* 2016), indicating both were resident tigers with established home ranges. That they abruptly

disappeared from the survey areas within NEPL after 2013 suggests they were killed, rather than they dispersed from the site or somehow remained at the site undetected during surveys in subsequent years. Therefore, I concluded that the management practices of the previous decade have failed to prevent the losses of large felids in the NEPL landscape and, more widely, throughout the country. With tiger and leopard fading out of the landscape, I found clouded leopard *Neofelis nebulosa* to be the most common large carnivore, followed by dhole *Cuon alpinus* and Asian golden cat *Catopuma temminckii*. Consequently, these three species emerged as a priority for further monitoring and conservation in the NEPL landscape. I also found that the leopard cat *Prionailurus bengalensis* and marbled cat *Pardofelis marmorata* have increased based on the comparison with surveys in 2003-2005 (Johnson *et al.* (2009), which may have been related to the increase in detection of small rodents compared to a decade earlier.

Among the ungulate prey species, northern red muntjac *Mutiacus vaginalis* was found to be the most common, followed by Eurasian wild pig *Sus scrofa*, Indochinese serow *Capricornis milneedwardsii* and small dark muntjac(s) *M. rooseveltorum* complex. Sambar *Cervus unicolor* and gaur *Bos gaurus* were extremely rare, thus it seems possible that this also could have contributed to the decline of tiger considering the latter two ungulates can be their preferred prey (Andheria *et al.* 2007; Kumaraguru *et al.* 2011). That said, wild pig is overall the most preferred prey of tiger (Hayward *et al*. 2012), and wild pig remained abundant and widely distributed in NEPL, indicating tiger populations declined due to increases in poaching within NEPL (Johnson *et al*. 2016) rather than prey declines.

Stump-tailed macaque *Macaca arctoides* was the most common primate species, East Asian porcupine *Hystrix brachyuran* was the most common small mammal prey species, and silver pheasant was the most common bird species that was considered potential prey. Overall, we found that NEPL still contains various prey species but at the very low abundance. This could mean that the population of meso and small carnivores can potentially be negatively affected if the abundance of the prey species continue to decline. That said, because illegal snaring

appeared to cause the extirpation of tiger and leopard and appears to be responsible for the current declines of mesocarnivores, then snaring is also likely the main factor causing the decline of prey species in NEPL.

It is important to note that although my study indicated stumped-tailed macaque was the most common primate species, this could have been an artefact caused by our study design, which targeted ground-dwelling species that used trails. Thus, some arboreal or semi-arboreal species were very likely missed or detected at very low rates.

Density of meso and small carnivores in NEPL

My original intention for this study was to estimate the density of all hypercarnivores. However, I learned that in order to have the results that are comparable for all species, spatially explicit-capture recapture technique for unmarked species (Chandler and Royle 2013) was needed. Although the use of this technique allows densities of all species to be estimated without having to identify individuals, I learned that accuracy of the estimates would be compromised. Therefore, the density estimation was carried out only for species with unique pelage markings: clouded leopard, leopard cat and marbled cat. Mean (± SD) density estimates for all years were $2 \pm 0.30/100$ km^2 for clouded leopard, $2.00 \pm 0.30/100$ km^2 for leopard cat, and $3.5 \pm 0.70/100$ km^2 for marbled cat. For clouded leopard, the average of three annual density estimates from this study were within the range of density estimate reported for other parts of their range in Southeast Asia, suggesting that the population of clouded leopards in NEPL is still viable. For leopard cat and marbled cat, the density estimates from my study were the lowest ever reported for these species. This indicates that leopard cat was not as common in NEPL as initially thought. Although the density estimate for marbled cat in my study were relatively low, I speculate that NEPL likely has the highest density and population of this species in Laos,

considering the extremely low records of this species from other sites in the country (Coudrat *et al.* 2014).

My analysis indicated a declining trend in density across the study years for clouded leopard, leopard cat, and marbled cat, with a stronger rate of decline for clouded leopard and leopard cat. I conclude that snaring, the factor that led to the extirpation of tiger and leopard in NEPL, is now likely contributing to the decline of smaller felids, and this factor likely overrode any potential effects of mesopredator release on their densities and interactions.

Spatial-temporal niche segregations of sympatric hypercarnivores

With an understanding that niche differentiation of coexisting species that are ecologically similar may occur in one or more niche dimensions, I aimed to investigate how five carnivore species (dhole, clouded leopard, Asian golden cat, leopard cat, and marbled cat) coexisted in the NEPL to insinuate the degree of their interactions. I used the multispecies occupancy modelling in Bayesian framework was to measure co-occurrence patterns between species and determine habitat factors influencing their occurrence. Additionally, I adopted the circular statistics and kernel density approaches to determine the diel activity patterns of each species and quantify the temporal overlap between species in the selected pairs.

Here I found that dhole presence did not influence clouded leopard and Asian golden cat occupancy, meaning no clear sign of avoidance or attraction. There was a slight positive association between clouded leopard presence and Asian golden cat occupancy, meaning there was some moderate degree of spatial overlap between the species. The Asian golden cat, leopard cat and marbled cat were more likely to use the same sites, meaning the degree of sympatry between the Asian golden cat and the two small felids was stronger than that between the Asian golden cat and the two mesopredators. However, the relationships between clouded

leopard and the two small felids, and that between dhole and the small felids were not tested because I assumed the competition among them would be minimal judging from their presumed lack of dietary overlap.

Dhole occurrence was positively associated with density of settlement areas but avoided habitat mosaic areas. I speculated that the attraction to human settlements by dhole was due to livestock raising areas adjacent to villages in and around NEPL. Chapter 1 showed that large ungulates like gaur and sambar (main prey species, as found by Kamler *et al.* 2012) were rare, therefore dhole may move closer to livestock grazing areas to consume large prey, which was supported by other studies (Cohen *et al.* 1978; Duckworth *et al.* 1999b; Aryal *et al.* 2015). Dhole's avoidance of habitat mosaic areas could be that this prefers areas with thick vegetation, which could be more advantageous for stalking and ambushing prey rather than more open areas (Karwanishi and Sunquist 2008).

The clouded leopard was positively correlated with more tree cover as well as grassland which was consistent with previous studies that showed a strong preference for forest habitats and also detected in grasslands (Nowell and Jackson 1996; Grassman *et al.* 2005a; Austin *et al.* 2007; Grassman *et al.* 2015; Hearn *et al.* 2018b). Clouded leopard was also found to have a positive association with roughness which could be due to its positive association with serow occurrence and its mechanism to avoid direct encounter with dhole. According to Kamler *et al.* (2012), dhole did not prefer serow, thus clouded leopard would have little competition when preying on this prey species.

The temporal activity overlap was low between dhole and clouded leopard. The dhole was mostly diurnal with activities peak at dawn and its activity highly overlapped with that of dark muntjac(s) and Eurasian wild pig. The peak of dhole's activity at dawn coincided with the most active hours of muntjacs. The clouded leopard had crepuscular activity patterns that peaked at dawn. The clouded leopard activity highly overlapped with that of the Indochinese serow and

sambar, which presumably are their potential prey. Therefore, prey specialisations might assist co-existence of dhole and clouded leopard.

The Asian golden cat was positively associated with both open and closed habitats which supports the previous speculation that they are habitat generalist, and is consistent with previous studies (Wang (2007b); Lyngdoh *et al.* (2011). The species was found to be active both day and night but with activity peaking at dawn. Its temporal overlap with dhole was not very high; most of the overlap was distributed around daylight hours. Asian golden cat activity overlapped more with that of the clouded leopard as activities of both species peaked at dawn. Asian golden cat activities highly overlapped with small-sized prey species such as muntjac, squirrels and silver pheasant. I concluded that being cathemeral is one of the co-existing mechanisms used by Asian golden cat to maximize the use of available resources in the same areas where fiercer competitors were present.

Although none of the habitat factors were shown to strongly influence leopard cat and marbled cat occurrence, based on strong positive association between the Asian golden cat and the leopard cat, I inferred that leopard cat occur in the same habitat types as Asian golden cat, which includes both open and closed habitats. This inference is supported by previous studies in Laos (Duckworth *et al.* 1999b; Johnson *et al.* 2009), Thailand (Grassman *et al.* 2005a; Lynam *et al.* 2013), and Borneo (Mathai *et al.* 2010; Mohamed *et al.* 2013a; Mohamed *et al.* 2016; Hearn *et al.* 2018b). The fact that my occupancy analysis results showed a slightly lower strength of association between Asian golden cat and marbled cat, compared to that of Asian golden cat and leopard cat, suggests a slight difference in marbled cat habitat use. It could be that the marbled cat specialised more on forest habitats as previously reported (Macdonald and Loveridge 2010).

Activity patterns of Asian golden cat overlapped more with that of marbled cat than with that of leopard cat. The marbled cat was primarily diurnal and had high overlap in activity with

potential avian and arboreal prey. It is possible that the marbled cat may specialise on these types of prey species rather than terrestrial small mammals to co-exist with the Asian golden cat.

The leopard cat was strongly nocturnal and was strongly correlated with murid activity. It was clear that leopard cat co-existed with Asian golden cat via temporal differentiation. For leopard cat, based on their low activity overlap with marbled cat and high activity overlap with potential prey, I conclude that leopard cat co-occurred with marbled cat via prey specialisation and temporal avoidance.

Carnivore conservation landscape

Using the results from species interaction (single-season, multi-species occupancy) modelling in Chapter 4, predictive maps of habitat suitability were created for the whole country to support conservation initiatives for medium-sized felids (clouded leopard and Asian golden cat) and dhole. Given the extent of their habitat requirements, and that they are largest hypercarnivores remaining in the country, I believe that successful conservation of these species will greatly benefit the conservation of smaller carnivores and their prey. The main prediction that most of the National Protected Areas (NPA) would represent suitable habitat for the three carnivores was not strongly supported by the findings from this study. The NPAs that are most actively managed and that receive comprehensive, long-term management support include: Nam Phouiy, Nam Kan, Nam Ha, NEPL, Phou Khao Khouay, Nam Kading, Phou Hinpoun and Nakai-Nam Theun. Although the suitable habitat for all three species appears mismatched with these areas at a meta level, there does remain some suitable habitat patches within these NPAs and the active management of these areas means these patches retain an important function as refuges (where threats to habitat loss occur at lower rates than non-protected areas) for the key species. This study mainly highlights importance of the National Protection Forest Areas

(NPFA) for the conservation of carnivore species in the country, especially in the northern provinces and along the central Annamite mountain landscape.

Practical application

Application of this study can be broken down into two aspects – study approaches and findings.

Application of study approaches:

- Despite intense efforts, camera trap surveys of cryptic and rare mammals in most cases yield sparse data. These datasets often are not analysed because they are considered to be insufficient for advance statistical analysis. Also, data collected from multiple seasons that are inconsistent in survey length between seasons are found to be difficult to integrate for a population dynamics study. The dynamic multispecies occupancy model in Bayesian framework that was adapted from Dorazio and Royle (2005) and Dorazio *et al.* (2006; 2010) for Chapter 2 provides a flexible analytical framework for the incorporation of such sparse, inconsistent yet valuable data on multiple species to assess their status via occupancy as a state process, offering scope to infer population dynamics over time.
- The adjusted density estimation (based on Spatially Explicit Capture Recapture model) framework (Gardner *et al.* 2010b) employed for Chapter 3 is applicable for estimating density of multiple species and of separate sessions (e.g., years or seasons) at the same time. The estimated density results from this type of analysis can then be used to estimate density trends over a period of time. Additionally, the original open population modelling framework by Gardner *et al.* (2010) allows aggregation of data from multiple years to assess demographic parameters (i.e., survival and recruitment rate). This type of information is crucial for population management of target species.

- The Bayesian multispecies-occupancy modelling framework adapted from Waddle *et al.* (2010) for Chapter 4 and 5 is a useful and flexible approach for estimating co-occurrence of interacting species. The same study approach can be applied to assess inter-specific interactions of different group of carnivore species or for examining predator and prey relationships (e.g., predator effects on prey detectability).
- GIS based predictive modelling used in Chapter 5 is another flexible framework that allows an integration of results from occupancy modelling, to model the distribution of suitable habit beyond our survey area for one or more species. This approach can be used to answer questions of "where?" and "how large of an area?" for species conservation planning. Additionally, human impacts on a landscape can be modelled and integrated into species habitat suitability modelling.

Application of findings:

- Chapter 2 provides the most recent assessment if animal diversity and status in the NEPL, Lao PDR. Regrettably, this most up-to-date assessment indicates that tiger and leopard have been extirpated from NEPL, and consequently extirpated from the entire country. In addition to considering whether tiger and leopard could be reintroduced, attention should focus on the conservation requirements of the clouded leopard and dhole, because both now have the potential to act as ambassador species for conservation in NEPL and throughout the country.
- Chapter 3 provided the first insights into populations of the clouded leopard, leopard cat and marbled cat in Laos where indiscriminate snaring is increasingly posting a major threat to wildlife conservation. Basic information such as density trends is of paramount importance, because assessment of conservation effectiveness can be enhanced through an understanding of population status, particularly changes in density over time. Given that findings from this study indicated a downward trend in the populations of the clouded leopard, leopard cat and marbled cat in NEPL, and that snaring was believed to

be responsible, the conservation of these species can benefit from snare removal and prevention through engagement and education of local people. Previous research in Southeast Asia showed that community engagement can contribute to a decrease in poaching (Steinmetz *et al.* 2014), therefore similar strategies should be attempted in NEPL in order to save the threatened species of felids remaining in the area.

- Chapter 4 provides one of the few detailed studies available in the region (Grassman 2004; Karwanishi and Sunquist 2008; Lynam *et al.* 2013; Sunarto *et al.* 2015) that looked at both felid and canid communities to capture a fuller picture of interspecific interactions. This is also the first detailed study that provided insights into the ecology of felid and canid communities in the NEPL as well as in the whole of Laos. For the species about which so little is known, such as the Asian golden cat and marbled cat, the findings add to the pool of knowledge and understanding of their ecology which are important for their conservation, especially since most of these species are listed as Threatened or Near Threatened by the IUCN. Our findings in terms of factors influencing species spatial distribution can further be used to produce predictive map that can benefit conservation planning.
- Findings from Chapter 5 showed suitable habitat of three hypercarnivores concentrating in northern part of Laos and within the central Annamite mountain region, and which was mostly distributed beyond the boundaries of NPAs but within NPFAs. This suggests further research should be focused in NPFAs prior to a development of a conservation plan, because such areas should not only be considered for watershed protection but also for biodiversity protection. Conservation in such areas may require strong community engagement because the NPFAs seem to have much higher density of human settlement than in and around most NPAs across the country.

Recommendations for further research

Future research should consider the following:

- Explore options to estimate density of species without individual recognition using camera trap data (Evans and Rittenhouse; Howe *et al.* 2017; Moeller *et al.* 2018; Nakashima *et al.* 2018), such as Asian golden cat and dhole. This will allow for the density estimation of all species within a specific area.
- The dynamic occupancy modelling for multispecies (as use for Chapter 2) should consider including habitat covariates to assess factors affecting occupancy of each species, while at the same time assessing factors that influence species richness.
- Habitat covariates for occupancy modelling should be extracted in multiple scales for each species because scales are important for understanding ecological patterns and processes (Kre *et al.* 2009; Razgour *et al.* 2011). While some species distribution may be explained by a large scaled landscape patterns, smaller scaled habitat patterns may better explain the distribution of other species.
- Dietary study should be carried out for the target species because this is important for making inferences about their inter-specific interactions.
- Seasonal interactions should be investigated because the species may have different level of interactions depending on seasonal change in resource availability (Boyer *et al.* 2003).
- Prey species distribution should be mapped and integrated into the carnivore habitat suitability models. With this integration, not only the associations between predator and prey can be inferred, but important prey hotspots also can be identified. In order to increase accuracy in habitat suitability prediction, more data sets from other camera trap studies across the country should be integrated.

- Further studies should consider extending my analysis based on habitat suitability modelling to also look at landscape connectivity, which includes defining core habitat areas and important corridors linking core areas for species' conservation. Knowing the locations of core areas and their linkages can help to raise awareness of these areas for carnivore conservation.

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