

Investigating carnivore guild structure: Spatial and temporal relationships amongst threatened felids in Myanmar

Pyae Phyoe Kyaw^{1,2*}, David W. Macdonald^{1*}, Ugyen Penjor^{1,3}, Saw Htun², Hla Naing², Dawn Burnham¹, Żaneta M. Kaszta¹, Samuel A. Cushman^{1,4}

¹ Wildlife Conservation Research Unit, Department of Zoology, The Recanti-Kaplan Centre, University of Oxford, Tubney House, Tubney, OX13 5QL, UK

² Wildlife Conservation Society Myanmar Program, Yangon, Myanmar

³ Nature Conservation Division, Department of Forests and Park Services, Taba, Thimphu, Bhutan

⁴ US Forest Service, Center for Landscape Science, Rocky Mountain Research Station, Flagstaff, AZ, USA

* Joint first authors

Correspondence

Pyae Phyoe Kyaw, Wildlife Conservation Society Myanmar, Yangon, Myanmar.

Email: pyaephyoekyawwcs@gmail.com

Abstract

At least nine felid species can co-occur in Southeast Asia, thus providing an unusual opportunity to investigate poorly known guild structure and the factors controlling it. Using camera-trap data, we quantified space use, temporal activity, and multi-dimensional niche overlap of tiger, clouded leopard, marbled cat, leopard cat, and Asiatic golden cat in Htamanthi Wildlife Sanctuary of Myanmar. We hypothesized that the spatio-temporal behaviour of smaller cats can reflect avoidance of the larger cats, which are both potential competitors and predators, and similar-sized guild members would partition their niches in space or time to reduce competition for resources. Our approach involved single-species occupancy modelling to identify site covariates, pairwise spatial overlap using Bayesian inference, and activity overlap with Kernel density estimation and multivariate analyses to test hypotheses. We found tiger and marbled cats were primarily diurnal, clouded leopard and leopard cat were nocturnal and golden cat exhibited cathemeral activity. We observed a complex pattern of guild assembly and potential competition involving strong niche displacement between the golden cat and marbled cat, but high overlap between the relatively similarly-sized pairing of clouded leopard and golden cat, and the markedly differently-sized tiger – golden cat pairing. No significant evidence of mesopredator release was observed and the felid assembly in Northern Myanmar appeared to be partitioned mainly on a spatial, rather than temporal, dimension. Nonetheless, the temporal association between the three mesopredators was inversely related to the similarity in their body sizes. The insights into this felid guild revealed that the largest niche differences in the use of space and time occurred between the three smaller species, most evidently between the Asiatic golden cat-marbled cat pairing, followed by marbled cat - leopard cat pairing. This study offers new insight into carnivore guild assembly and, adds substantially to knowledge of five of the least known felids of conservation concern.

KEYWORDS

activity pattern, co-occurrence, Htamanthi Wildlife Sanctuary, multi-species occupancy, niche partitioning

1. Introduction

The science of ecology is underpinned by niche theory (Hutchinson, 1957). This theory postulates that the distribution, abundance, and survival of organisms is dictated by their ecological niche, defined as a function of limited resources within an n-dimensional hypervolume of multiple environmental variables (Blonder, 2018; Hegel et al., 2010). However, quantifying species' ecological niches, even for well-studied species, is rarely straightforward (Mayor et al., 2009). In particular, species interactions among predator-prey and competitor species networks may influence species distribution and abundance, and interact strongly with environmental dimensions of the ecological niche. Therefore, niche analysis should account for both environmental and biotic interactions and attempt to quantify the relationships among them.

The assembly of ecological communities is a fundamental topic in ecology. Amongst mammals, guilds of carnivores have been particularly useful in understanding drivers of community and guild structure in relation to, for example, character displacement and niche partitioning (Dayan et al., 1989; Hearn et al., 2018; Macdonald et al., 2017; Macdonald & Sillero-zubiri, 2004) and intra-guild hostility (Macdonald et al., 2010, 2017; Macdonald & Sillero-zubiri, 2004). Among carnivore taxa, the Felidae offer a particularly relevant model system for understanding niche separation and apparent competition given that all 37 species are very similar in morphology and behaviour, differing principally in size, and since they occur in many different combinations of species' assembly (Macdonald & Loveridge, 2010).

The combinations of felid species in different communities offer the opportunity to test how a guild functions in the presence and absence of different component species. For example, Oliveira et al. (2010) describe niche relationships among 11 sympatric neotropical felid species in South America. Their study observed the possible mesopredator release (Crooks & Soule, 1999) among neotropical felids since ocelot (*Leopardus pardalis*) density is not affected by larger species such as puma (*Leopardus pardalis*) and jaguar (*Panthera onca*) but smaller cats exhibited higher densities as ocelot numbers decrease or in areas where ocelots are not found. A very similar guild, with highly convergent members paralleling those in the Americas, is comprised of up to 12 felid species in Southeast Asia (Macdonald & Loveridge, 2010). Hearn et al. (2018) modelled spatial and temporal niche structure and partitioning among three Southeast Asian felid species and found clear patterns of displacement related to body size and likely prey preferences in terms of spatial and temporal niche structure. Specifically, (Hearn et al., 2018) found that smaller felids tend to be separated spatio-temporally from larger mesopredators such as clouded leopards (*Neofelis diardi*), but may, as illustrated by the small marbled cat (*Pardofelis marmorata*), exhibit broad-scale habitat overlap with clouded leopards while, on a finer scale, strongly avoiding them.

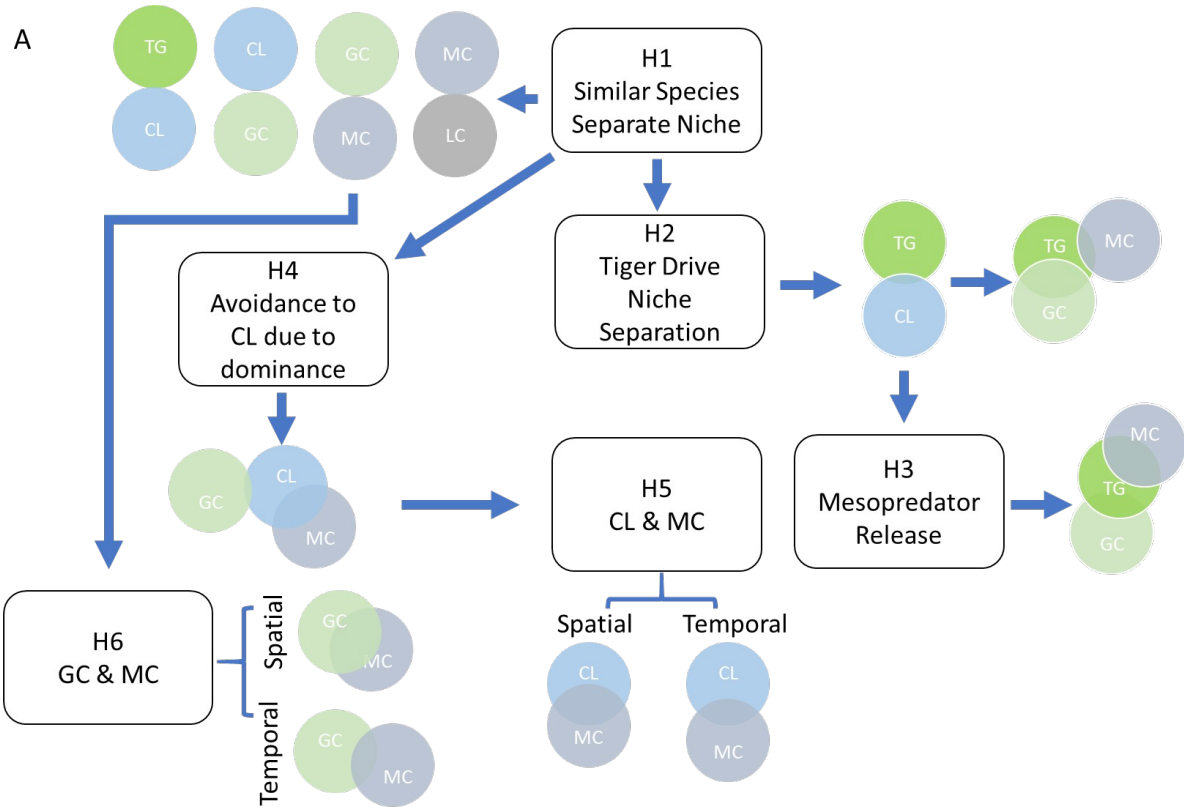
Building on the results of these studies we aim to explore the patterns and potential drivers of felid niche overlap among multiple species in the Htamanthi Wildlife Sanctuary (HWS) of the Northern Forest Complex (NFC) of Myanmar (Figure 2), where seven felid species co-exist: the tiger, *Panthera tigris* (Endangered), mainland clouded leopard, *Neofelis nebulosa* (Vulnerable), Asiatic golden cat, *Catopuma teminikii* (Near Threatened), marbled cat, *Pardofelis marmorata* (Near Threatened), common leopard, *Panthera pardus* (Vulnerable), the jungle cat, *Felis chaus* (Least Concern), and the leopard cat, *Prionailurus bengalensis* (Least Concern). The area is also important for transboundary biodiversity

habitat conservation since it lies at the confluence of three biodiversity hotspots: Himalaya, Mountains of Southwest China, and Indo-Burma (Myers et al., 2000), and is a critical node for regional wildlife connectivity (Kaszta, Cushman, & Macdonald, 2020). In addition, research and conservation activities are increasingly shifting from single species to guild and multi-species investigations (e.g. Estes, 1996; Caro, 2007; Hearn et al., 2018), not only to better understand the interaction between species but also to better support conservation. Therefore, our objective was to explore intra-guild interactions among mesopredators (clouded leopard, marbled cat, Asiatic golden cat, leopard cat), and the much larger tiger in the Htamanthi Wildlife Sanctuary. -

This study is a component of a region-wide research program centred on clouded leopard (Kaszta et al., 2020; Macdonald et al., 2019) and the felids with which they co-occur in an aggregated range running from Nepal in the west (Can et al., 2020) to Kalimantan in the southeast (Cheyne & Macdonald, 2011). Within this region, several past studies have described aspects of the felid guild, such as the population densities, habitat use and demographics of various member species (Ash, Hallam, et al., 2020; Can et al., 2020; Naing et al., 2019; Penjor et al., 2018; Rasphone et al., 2019; Tan et al., 2017). There have been few studies focused explicitly on species interactions within the felid guild, most of which addressed particular pair-wise interspecific interactions (Haidir et al., 2013, 2018; Hearn et al., 2018; Singh & Macdonald, 2017). Although studies of competition, interactions and resource partitioning of sympatric Asiatic felids are accumulating (Haidir et al., 2018; Hearn et al., 2018; Odden et al., 2010), how different-sized members of this felid guild respond to each other is still poorly known and this was a motivation for our study. From previous studies (e.g., Hearn et al., 2018; Oliveira et al., 2010) there seems to be a general pattern of niche displacement in time and space in which species of similar size tend to show the largest niche displacement, and dominant predators, such as tiger, often also displace mesopredators and perhaps also suppress competition between some mesopredators. Therefore, we hypothesize that larger cats can influence the spatial and temporal niches of smaller cat species, due to predation and interference competition, leading to displacement of realized niches in time and space. We expected that coexistence of the felid guild would be mediated by behavioural mechanisms such as segregation of space use and temporal activity pattern (Hearn et al., 2018).

Specifically, we had six hypotheses based on body size relationships between the species (Figure 1 A and B). (1) We expected that niche separation in spatial and temporal niche dimensions, and their intersection, would be associated with difference in body size, such that similarly-sized species would occupy more distinct ecological niches, given their expected higher likelihood of interference competition. (2) We expected that clouded leopard, golden cat and marbled cat would show spatial or temporal displacement from tiger, with clouded leopard showing the largest displacement, followed by golden cat and finally marbled cat. This is based on the expectation that tiger, as the dominant member of the guild, could drive niche separation in this system, with the species most similar in body size to tiger expressing the largest displacement. (3) We hypothesized that there could be mesopredator release of golden cat and marbled cat arising from displacement of clouded leopard by tigers, in which case we would expect low overlap between tiger and clouded leopard, but higher overlap between golden cat and marbled cat with tiger. (4) We also expected niche displacement of both golden cat and marbled cat as both sought to avoid the competitively superior clouded leopard, either spatially or temporally, and we expected this displacement to be more marked for the golden cat because of its

126 more similar size to the clouded leopard. (5) Following Hearn et al. (2018), who characterised the Sunda
 127 clouded leopard as nocturnal and the marbled cat as diurnal, we expected the displacement between
 128 marbled cat and clouded leopard to be primarily temporal and therefore hypothesized that these
 129 species may utilize the same areas but at different times of day without experiencing elevated
 130 competition between them. Finally, (6) we predicted that marbled cat would show the strongest
 131 displacement with golden cat, to which it is most similar in size; furthermore, the marbled cat has been
 132 documented to be diurnal and the golden cat to be more cathemeral, so we expected any displacement
 133 to be primarily be in the temporal niche dimension. Each hypothesis expresses the expected outcomes
 134 of particular interactions between subsets of the guild, assuming all else is equal. However, in nature we
 135 expect complicated, cascading, interactions between these processes. Therefore, we employ a
 136 multivariate analysis approach that evaluates support for each hypothesis individually and all
 137 hypotheses in combination with each other. This enables us to evaluate the pattern of niche separation
 138 across multiple potentially interacting hypotheses of niche differentiation in the felid guild of northern
 139 Myanmar.



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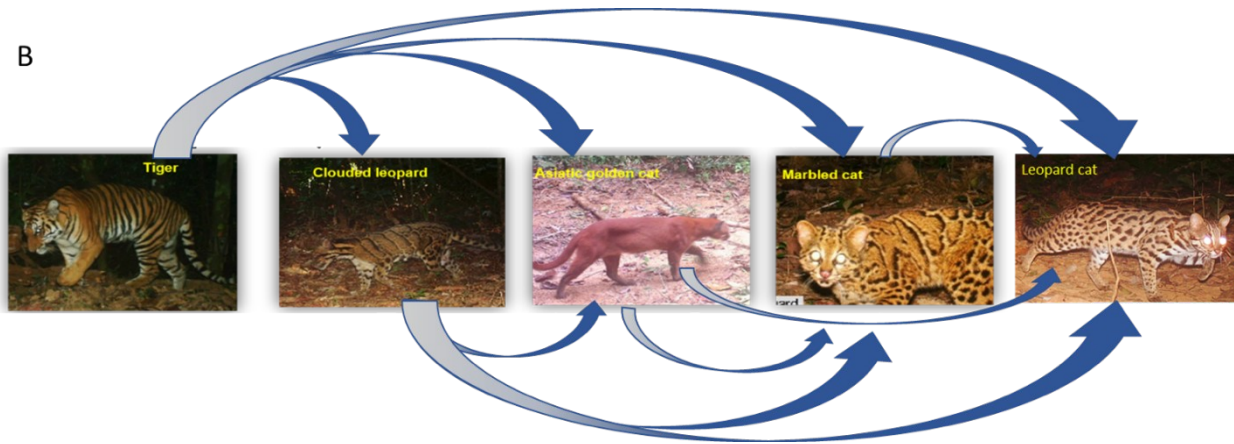


FIGURE 1 (A) Proposed hypotheses of spatio-temporal interaction among felid species. (where TG=Tiger, CL= Clouded leopard, GC=Asiatic golden cat, MC=Marbled cat and LC=Leopard cat, H= Hypothesis. The amount of overlap of circles represent greater or lesser spatio-temporal overlap between two species). (B) Proposed model of spatio-temporal influence of larger cats on smaller cat (from left to right: tiger (*Panthera tigris*), clouded leopard (*Neofelis nebulosa*), Asiatic golden cat (*Catopuma teminckii*), Marbled cat (*Pardofelis marmorata*) and leopard cat (*Prionailurus bengalensis*) (photos not to scale)

2. Materials and Methods

2.1 Study Area

The data were collected during camera trap surveys in the Htamanthi Wildlife Sanctuary (HWS) of Myanmar, Southeast Asia (Figure 2), which is the largest protected area in the Sagaing Region of Myanmar (2151 km²). The elevation of HWS ranges from 141 meters to 618 meters, with small undulating hills throughout. Forest types in HWS include semi-evergreen, moist and dry mixed deciduous forests (Arino et al., 2012). A high diversity of threatened Asian large mammal species inhabit HWS, including tiger, dhole (*Cuon alpinus*), Asiatic black bear (*Ursus thibetanus*), Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), and, previously, Sumatran rhino (*Dicerorhinus sumatrensis*) (Hundley, 1952; cited in Rabinowitz, Schaller, & Uga, 1995). The eastern and western borders of the HWS abut rural communities. The sanctuary was being considered for a dam construction project, and consequently was being exploited by logging companies until 2012. After that project was cancelled, numerous threats remain (e.g., poaching, illegal logging, and artisanal gold mining). For law enforcement and management purposes, the sanctuary is divided into four management zones from north to south, namely: Nam Phi Lin, Nam E Zu, Nam Pa Gon, and Nam Yan Yin (Figure 2).

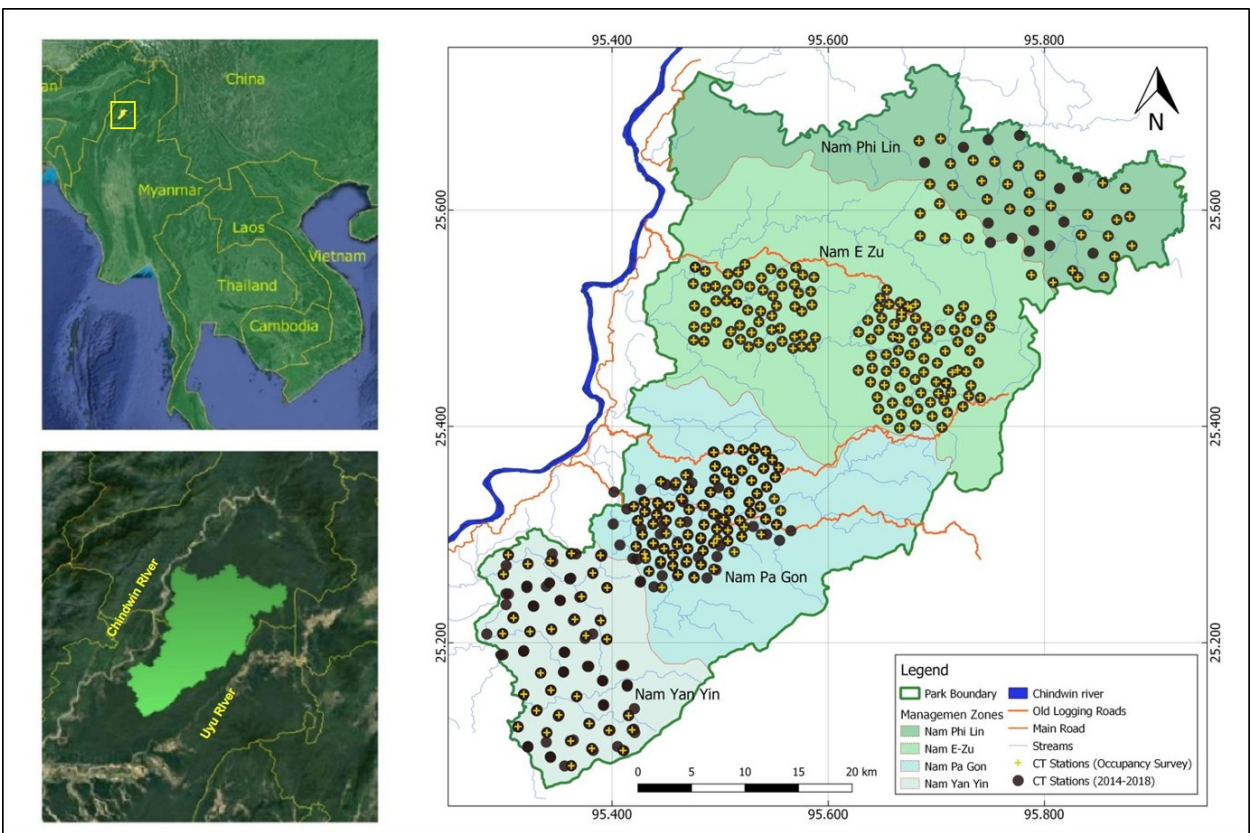


FIGURE 2 Camera trap surveys in Htamanthi Wildlife Sanctuary. A total of 525 camera trap stations (black dots) has been deployed and surveyed across the sanctuary (2014-2018). 288 camera stations (yellow stars) were use in space use analysis

2.2 Camera trap surveys

Camera trap surveys were undertaken from 2014 to 2018. These surveys were conducted by the Nature and Wildlife Conservation Division of the Forest Department and the Wildlife Conservation Society Myanmar in collaboration with the Wildlife Conservation Research Unit (WildCRU) of the University of Oxford, International Union for Conservation of Nature (IUCN) and Foundation Segre. Each year, survey areas were selected for each survey to avoid spatial overlap of camera grids, and to maximize the inter-annual coverage. In total, five survey grids were monitored with seven surveys in the HWS. Due to some differences in target species, and procedures, between surveys, there were variations in the numbers of camera stations and trapping duration, but overall spacing between each camera stations ranged from 319 meters to 2528 meters (mean= 1324.9 with SE±27.01). Except for that targeting sun bears, all surveys used paired camera traps at each station (Table S1 in supporting information documents the details of numbers of planned and working camera stations, and target species for each survey).

Camera trap image metadata extraction was carried out using the “Exif file extractor” (BRSoftware, 2012) and the “Panthera camera trap file manager” software (Olliff et al., 2013; PantheraCameraTrap, 2012). Animals photographed were identified manually and tagged with relevant metadata. From 2017, a camera trap data management and analysis package (CTAP), developed by Zoological Society of London (ZSL) (Davey et al., 2015), was used to compile and summarize yearly camera trap data. The non-uniformities in date and time formats, species names and field surveys were also standardized using the CTAP package in ZSL software. We excluded common leopard and jungle cat from our model since only two leopard individuals and one photo of a jungle cat were observed in our survey.

2.3 Space use and species interaction

From a total of 525 camera trap stations, we excluded 32 faulty stations and 205 stations surveyed repeatedly as in this analysis, to conform with single-season model, we used only those stations that were surveyed once. The remaining 288 were chosen for space use analysis. Occupancy modelling assumes closure of populations (MacKenzie et al., 2002), whereas our analyses amalgamate data from surveys in different years and different sectors of the study site. Furthermore, since different surveys targeted different species (tiger, clouded leopard, sun bear) in different sites, the criteria of independence between sites, and of spatial autocorrelation, might also be violated. However, these assumptions are all relaxed when occupancy is interpreted as a “probability of space use” (MacKenzie et al., 2017). Although our main objective is to estimate the interaction between the five felid species over space use, we nonetheless applied an initial occupancy modelling framework to identify the most meaningful set of covariates affecting the probabilities of individual species’ space use (Methods S1 and Figure S1 documents how this was done by single-species occupancy modelling, and presents the model outcomes).

Figure 3 presents the workflow used to estimate space use and spatial interactions between felids. We first estimated the overlap in space use of the five felid species using multi-species occupancy modelling based on Bayesian inference (Waddle et al., 2010). Our multi-species model assumed asymmetric interaction between dominant and subordinate species, where the presence of subordinate

species is dependent on the presence of dominant species but not *vice versa* (Waddle et al., 2010). Our model includes the following interactions: a) tiger habitat use affecting clouded leopard, marbled cat, Asian golden cat and leopard cat; b) clouded leopard affecting marbled cat, Asian golden cat and leopard cat; c) Asian golden cat affecting marbled cat, d) Asian golden cat and marbled cat affecting leopard cat (Figure 2B). Our model enables the simultaneous estimation of both space use and detection probability of multiple species while allowing for interspecific interactions, and allows us to model covariate effects otherwise impossible in previous models (e.g., Mackenzie et al., 2003). In this analysis, we estimated the overlap or avoidance of each pair of species, while accounting for possible interactions – an approach demonstrated to reveal biologically meaningful results (Bischof et al., 2014).

From single-species occupancy modelling (Method S1), we identified six covariates: distance to boundary, disturbance, elevation, tree cover, distance to main streams (used by boats) and density of streams which were used as site covariates in the multispecies model. For all species we modelled detection probability as a function of survey effort, and for all except tiger, we used all site covariates, whereas for tiger we used distance to boundary, disturbance, mean elevation and tree cover.

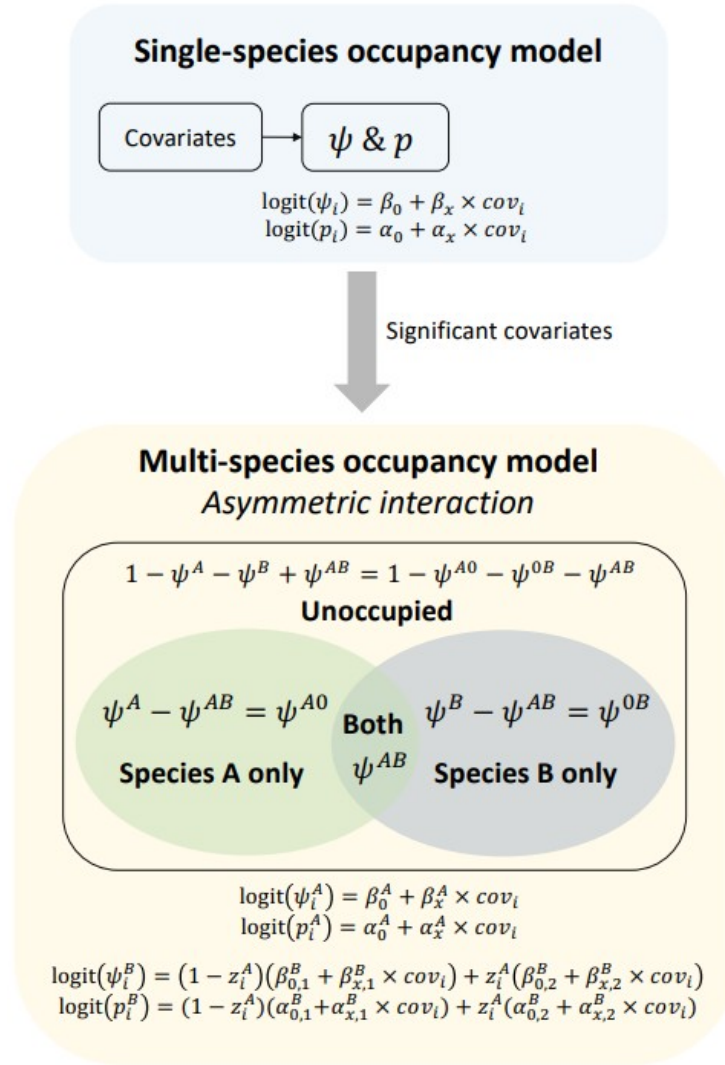


FIGURE 3 Workflow depicting single-species, single season model (top) and multi-species asymmetrical interaction occupancy model (bottom). Single-species occupancy models were used to identify best covariates for each species. Multi-species occupancy model was used to examine the probability for each occupancy state (coloured Venn diagrams). Green ellipse represents the probability the species A occupies a site irrespective of species B and grey ellipse represents the probability species B occupies the site irrespective of species A. The intersection represents the probability that the site is occupied by both species.

For priors of occupancy for interacting species, we used the normal distribution function (with mean=0, standard deviation=1.4) as suggested by Northrup & Gerber, (2018). Our sensitivity analyses with different values of SD indicated this prior to yield sensible estimates (Figure S2, Supporting information). To quantify overlap and avoidance, we used the log-odds and 95% credible interval of the posterior distribution of parameter estimates (Bischof et al., 2014; Haidir et al., 2018). We ran the model with four parallel chains of 300,000 Markov Chain Monte Carlo (MCMC) iterations each and discarded 50,000 as burn-in and thinning at the rate of 5 while allowing for chains to stabilize. We checked the

model convergence with \hat{R} values (the value of which <1.1 indicates convergence (Gelman et al., 2013) and MCMC trace plots (Gelman & Rubin, 1992). We used the “R2jags” package in R (R Core Team, 2013; Su & Yajima, 2015) to call JAGS (Plummer, 2003) to fit our models.

2.4 Temporal activity and overlap

Two different datasets were used to study overlap of temporal activity. Firstly, we pooled all the camera trap data obtained from all 493 working camera trap stations, of which 312 stations detected our study species. Secondly, we used the subset of data from the spatial analysis where 199 stations detected our study species. Therefore, we obtained two dataset containing different number of independent total observations for all species ($n=1344$ and $n=823$). Lynam et al. (2013) advised caution in interpreting results of temporal overlap analysis from small surveys. Thus, we analysed both datasets separately to compare activity pattern and overlap to check the representativeness of activity patterns. We assumed that individuals of each species had an equal chance of being photographed when they were active (Linkie & Ridout, 2011). A capture by camera was described as “activity” regardless of the behaviour which could be determined in the camera trap image. We regarded consecutive photographs of the same species at a station within 30 minutes as one event. The first detection in any 30-minute window was retained and considered independent. Based on local time, diurnal activity was defined as 07:00-17:59 and nocturnal activity as 20:00-04:59. Crepuscular activity was regarded as 05:00-06:59 (dawn) and 18:00-19:59 (dusk).

Diel activity was explored by comparing and overlapping the activity patterns of clouded leopards, tigers, marbled cats, Asiatic golden cats and leopard cats with kernel density plots (e.g., Hearn et al., 2018). Although histograms are widely used to estimate probability density functions, kernel estimators have the advantage of being intuitive to interpret, simple to analyse mathematically, and are more efficient (Wand & Jones, 1994; Hearn et al. 2018). Thus, we constructed Von Mises kernel density plots corresponding to the circular distribution of diel data. Since smoothing can affect estimation of activity overlap, we tested the sensitivity by using different bandwidth values ($c=1$, $c=0.5$ and $c=0.1$) and compared the bootstrap means and confidence intervals (Table S6 in supporting information). For overlap, we used ‘Dhat4’ estimator for species-pairs with sample size > 75 and, ‘Dhat1’ estimator for pairs including sample size < 75 were used (Meredith & Ridout, 2017). We obtained confidence intervals as percentiles from 10,000 bootstrap samples. All the statistical analyses were carried out using “overlap” package (Ridout & Linkie, 2009) in R (R Core Team, 2013).

2.5 Multi-dimensional spatio-temporal overlap

In addition to spatial and temporal overlap analyses, we also computed an index for multi-dimensional overlap. For each species, we multiplied the spatial overlap with the time overlap estimates to obtain the total overlap expected in space and time simultaneously. This gives the total overlap expected in space and time simultaneously (e.g. will the animal be active in the same place at the same time).

2.6 Multivariate Evaluation of Support for all Hypotheses

We used Mantel tests (Mantel, 1967) to evaluate the support for each hypothesis individually and all hypotheses in interaction. The Mantel test is a correlation between distance matrices. The dependent variable matrices in this test were the pairwise overlap matrices among the five species for overlap in (1) space, (2) time, and (3) jointly in space and time. The independent variable matrices were model matrices (Legendre & Legendre, 1998) representing the expectation of each hypothesis (Table S7). The correlation between the overlap observed among pairs of species and the expected pattern of dissimilarity among species in each hypothesis gives a quantitative measure of the support for each individual hypothesis. In addition, by computing the summed combinations of all model matrices among hypotheses we are able to test the joint support for multiple hypotheses simultaneously (e.g., Ash, Cushman, Macdonald, Redford, & Kaszta, 2020). We ranked combined hypotheses based on the magnitudes of the Mantel correlation (e.g., Cushman, McKelvey, Hayden, & Schwartz, 2006), and assessed statistical significance based on 100,000 matrix permutations (Legendre & Legendre, 1998).

3. Results

3.1 Space use

From a total of 288 camera trap stations, five felid species were detected in sufficient numbers to sustain spatial interaction analysis - tigers (31 stations), clouded leopard (98 stations), Asiatic golden cat (80 stations), marbled cat (52 stations) and leopard cat (75 stations). We estimated ten pair-wise intersections of space use between five sympatric felid species based on our single season modelling (Figure 4). Almost all species showed spatial interaction with each other. The leopard cat space use was highly associated (from 95% to 100% of overlap) with that of all the larger felids (Figure 4). Only marbled cat showed slight avoidance (58% overlap) with Asiatic golden cat. Marbled cat also showed weak avoidance of larger species (e.g. Asian golden cat, clouded leopard and tiger). The initial single species occupancy outputs (Table S2 , S3 and S4), the JAGs model output (Table S5), posterior distributions and associated uncertainties of the co-occurrence models (Figure S3) are detailed in supporting information.

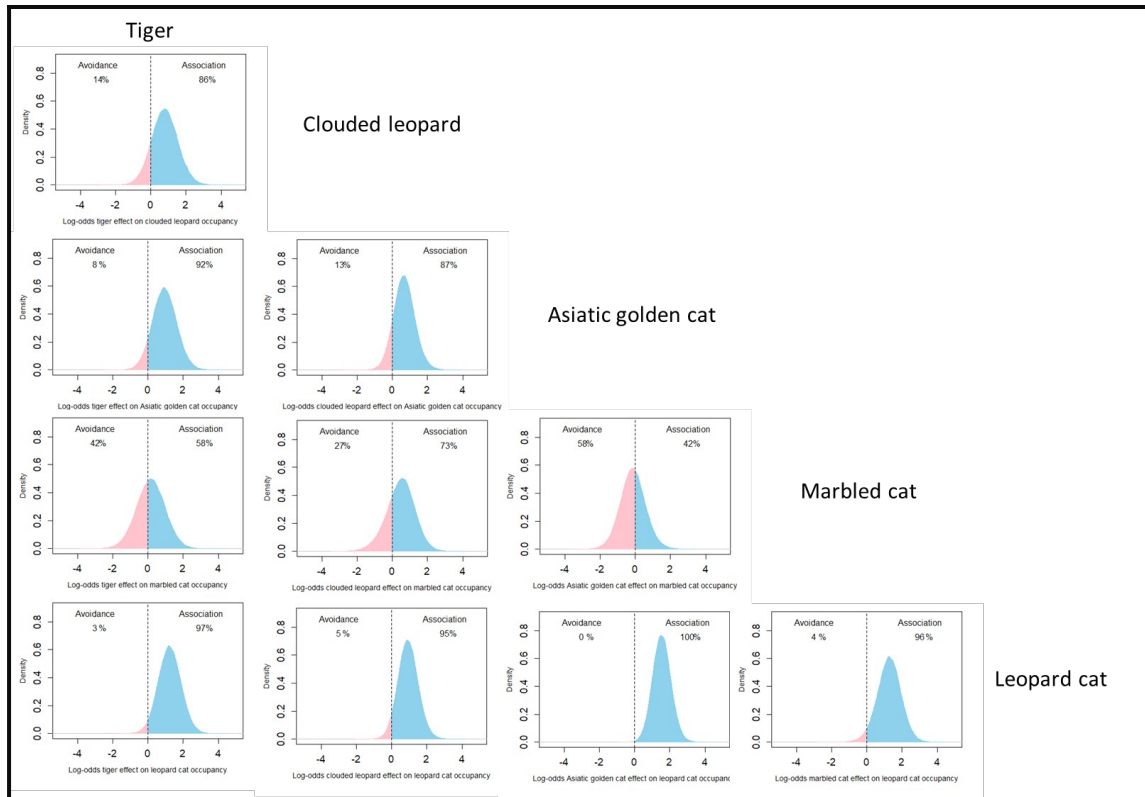


FIGURE 4 Spatial association and avoidance between tiger, clouded leopard, Asiatic golden cat, marbled cat and leopard cat based on multi-species spatial interaction model. This shows the log-odds ratio of dominant species to subordinate species (Blue shade: Probability of association, Pink shade: Probability of avoidance)

3.3 Activity Pattern and Temporal Overlap

Tiger and marbled cats were primarily diurnal in our study area (73% and 83%) while clouded leopards were mostly nocturnal (37% diurnal activity), with activity peaks observed around 0400 hours. Asiatic golden cat tended to be cathemeral, and were active during both night and day (45 % diurnal). The leopard cat was mostly nocturnal (51%) with highest peaks of activity peaks early in the night and before dawn. Table S7 tabulates a summary of the activity patterns revealed by our own study and others in neighbouring countries.

Tiger and marbled cat exhibited the most similar activity patterns of any pairing, with the highest coefficient of temporal overlap for both datasets ($\Delta_1=0.88$ for $n=823$ and $\Delta_4=0.89$ for $n=1344$) (Table 1 and Figure 5). The two smallest species, the marbled and leopard cats exhibited the strongest temporal segregation ($\Delta_4=0.27$ and $\Delta_4=0.29$), a difference likely resulting from their different diel activities. Also, leopard cat had low temporal overlap with tiger (Δ_1 and $\Delta_4=0.36$). Several pairings had relatively high overlaps in activity around the crepuscular periods of 6:00 and 18:00. Values for the overall overlap coefficient and in the activity patterns were similar for the two datasets ($n=1379$ and $n=844$) (Table 1). We validate our diagnoses through a comparison of diel activities calculated from the two datasets and overlap coefficient plot displayed in Figure S4 and Figure S5. Our findings concur with those in the literature for these same felids in different regions (Table S7).

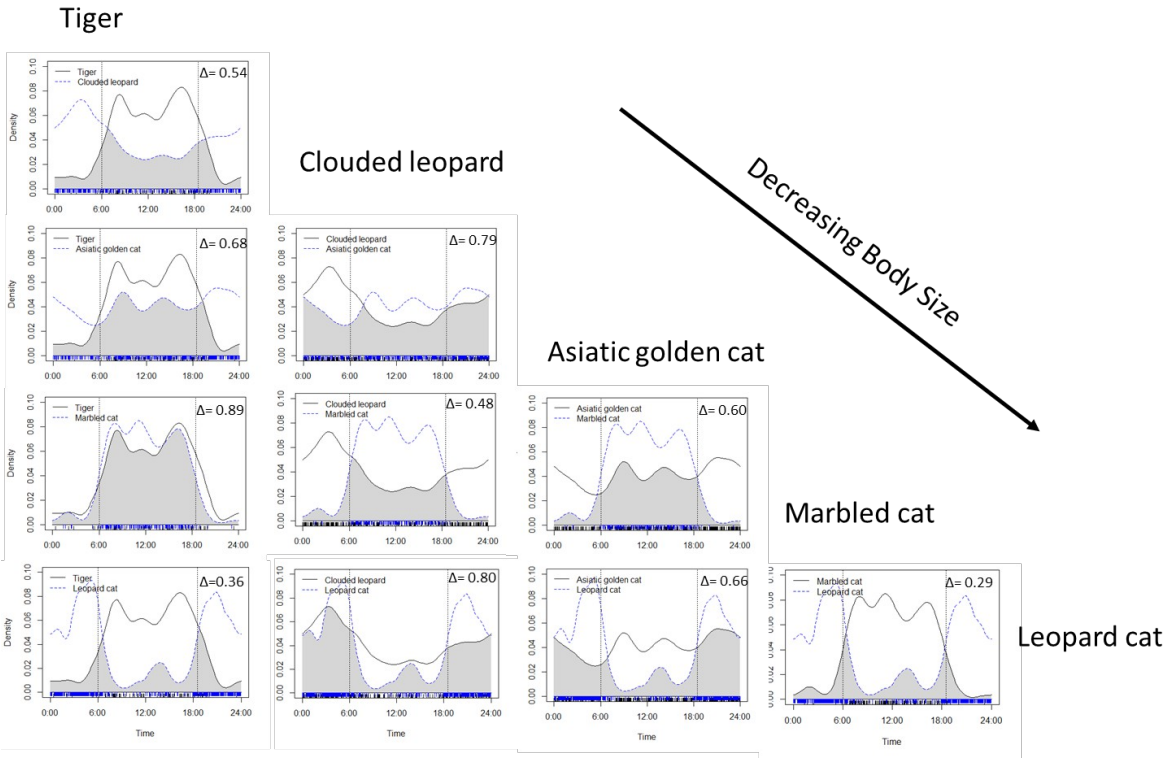
325 **TABLE 1** Coefficient of overlap in activity pattern of tiger, clouded leopard, marbled cat, Asiatic golden
 326 cat and leopard cat with 95% confidence intervals for both different sample sizes, n=823 (Δ_1) and n=1344
 327 (Δ_4)

	Clouded leopard		Asiatic golden cat		Marbled cat		Leopard cat	
	n= 823 (Δ_1)	n=1344 (Δ_4)	n= 823 (Δ_1)	n=1344 (Δ_4)	n= 823 (Δ_1)	n=1344 (Δ_4)	n= 823 (Δ_1)	n=1344 (Δ_4)
Tiger	0.6 (0.48-0.72)	0.54 (0.45-0.63)	0.68 (0.57-0.78)	0.68 (0.59-0.76)	0.88 (0.77-0.97)	0.89 (0.81-0.97)	0.36 (0.26-0.47)	0.362 (0.27-0.44)
Clouded leopard			0.83 (0.75-0.90)	0.79 (0.72-0.85)	0.525 (0.44-0.61)	0.48 (0.41-0.55)	0.73 (0.65-0.79)	0.79 (0.74-0.85)
Asiatic golden cat					0.59 (0.51-0.67)	0.60 (0.54-0.67)	0.64 (0.57-0.79)	0.664 (0.61-0.72)
Marbled cat							0.273 (0.20-0.35)	0.29 (0.24-0.36))

328

329 **3.4 Multi-dimensional Spatio-temporal Overlap**

330 We multiplied spatial overlap by temporal overlap, giving an index of multi-dimensional niche
 331 overlap between each combination of species (Table 2). Clouded leopard and leopard cat had the
 332 highest multi-dimensional niche intersection (0.76), followed by clouded leopard and golden cat (0.69).
 333 By far the lowest total intersection was between Asiatic golden cat and marbled cat (0.25). The two
 334 species most similar in size, the marbled and leopard cats also exhibited low intersection (0.28) as did, to
 335 a lesser extent, tiger-leopard and clouded leopard-marbled cat pairs (0.35).



336

FIGURE 5 Activity overlap of tiger, clouded leopard, marbled cat and Asiatic golden cat from all camera trap stations (n=1344). Dotted vertical lines at 06:00 and 18:00 hour represents the approximate dawn and dusk. Activities detected for each species are represented by blue and black coloured rugs on x axes

TABLE 2 Index of niche overlap: spatial, temporal and multidimensional overlap (index of niche overlap as a multiplication of spatial and temporal overlap) between each pair of species

Paired Species	Spatial Overlap	Temporal Overlap	Index of Niche Overlap
Tiger - Clouded leopard	0.86	0.54	0.46
Tiger - Asiatic golden cat	0.92	0.68	0.63
Tiger - Marbled cat	0.58	0.89	0.52
Tiger - Leopard cat	0.97	0.36	0.35
Clouded leopard - Asiatic golden cat	0.87	0.79	0.69
Clouded leopard - Marbled cat	0.73	0.48	0.35
Clouded leopard - Leopard cat	0.95	0.8	0.76
Asiatic golden cat - Marbled cat	0.42	0.6	0.25
Asiatic golden cat - Leopard cat	1	0.66	0.66
Marbled cat - Leopard cat	0.96	0.29	0.28

3.5 Multivariate Analysis of Hypothesis Support

We computed 64 combined hypotheses as the combinations of the six individual hypotheses articulated in the Introduction section. We evaluated support for each of these using Mantel tests between the pairwise overlap matrices in space, time and jointly in space and time among all pairs of species and the model matrix corresponding to that hypothesis (Table 3). For each of spatial, temporal or joint overlap we ranked the hypotheses by Mantel r value. We discuss only those that meet significance thresholds at three alpha levels (0.05, 0.1, 0.2). Given the low power in Mantel testing on small matrices, such as those resulting from the combination of only five species, the magnitude of the Mantel r statistic is likely more informative than significance testing (e.g., Cushman et al. 2014), and a more liberal alpha level is recommended when significance testing is used. We evaluate and discuss hypotheses that have support at the 0.2 alpha level, and also discuss those supported at 0.1 and 0.5 with increasing confidence.

For the analysis of the spatial overlap among felid occurrence, 16 combined hypotheses were significant at the 0.2 level, 9 at the 0.1 level and two were significant at 0.05. All of these had very large support based on the magnitude of the Mantel correlations, which was large ($M_r > 0.5$) and indicated strong linear relationship between the spatial overlap and the model matrices in these 16 hypotheses (Table 3, 4). Table 4 reports the proportion of supported models at each alpha level containing each of the 6 individual hypotheses. Hypothesis 6 is included in all supported hypotheses at all three alpha levels. Hypotheses 5, 4, 2 and 1 received partial support for partitioning on the spatial niche dimension, with 50% of models supported at alpha 0.2 including these hypotheses. Hypothesis 5 was included in all models supported at the 0.05 level and the most supported single hypothesis based on significance of support is the joint effect of hypothesis 5 and 6 on spatial overlap patterns among species. Hypothesis 3 was not included in any supported models at any significance level for spatial overlap, and hypothesis 4

was poorly supported at the higher significance levels (0.1 and 0.05). Hypothesis 2 was supported in half of the models supported at the highest (0.05) significance level.

No hypotheses were significant at the 0.2, 0.1 or 0.5 alpha thresholds for temporal overlap analysis (Table 3). No correlations between pairwise temporal overlap and any of the 64 model matrices were greater than 0.25, indicating weak relationships between patterns of temporal overlap among the activity patterns of the five pairs of species and any of the hypotheses independently or jointly.

In the analysis of the joint overlap in both spatial and temporal dimensions 14 models were supported at the 0.2 alpha level, four were supported at 0.1, and one was supported at 0.05 (Table 3). These had moderate support based on the magnitude of the Mantel correlation (all greater than 0.32), but none was as large as the largest Mantel correlations between the spatial dimension of overlap and niche displacement hypotheses (Table 3). Hypothesis 6 was included in all supported hypotheses at all three significance levels (Table 5). Hypothesis 5 was supported in the majority of models at the 0.2 alpha level and was included in the only temporal overlap model supported at the 0.05 level. Hypothesis 1 was also included in the temporal model supported at the 0.05 level. In contrast to the spatial overlap analysis, there was some, but weak support, for hypothesis 3 in the joint space-time overlap analysis (Table 5).

TABLE 3. Ranking support for joint niche separation hypotheses across spatial, temporal and combined dimensions. Hypotheses are ranked in order of Mantel correlation between niche overlap and the model matrix for each hypothesis. Space – hypotheses tested for spatial partitioning; Time – hypotheses tested for temporal partitioning, Both – hypotheses tested for the joint partitioning of Space*Time.

	Space		Time		Both
h6	0.744039	h521	0.249662	h56	0.559339
h61	0.701492	h52	0.243368	h561	0.552768
h56	0.689977	h21	0.210831	h563	0.479433
h561	0.678573	h2	0.203053	h5631	0.471467
h562	0.653961	h5621	0.183776	h6	0.468506
h5621	0.641009	h562	0.18278	h61	0.45542
h642	0.573308	h621	0.133527	h5632	0.401457
h62	0.568964	h62	0.128445	h63	0.39911
h5642	0.568784	h51	0.112882	h65132	0.39616
h621	0.56005	h5	0.092942	h631	0.393296
h64	0.559176	h5321	0.081704	h5621	0.385264
h65412	0.551393	h1	0.078137	h562	0.381349
h6421	0.540358	h532	0.075186	h5643	0.325979
h641	0.53192	h65132	0.049103	h65431	0.325704
h564	0.5058	h5421	0.046912	h51	0.317474
h5641	0.501893	h321	0.045872	h531	0.316421
h65132	0.281248	h5632	0.041761	h53	0.308404
h5632	0.274345	h32	0.036733	h6321	0.29811
h654321	0.258631	h542	0.035303	h632	0.296964

h5631	0.258607	h561	0.032644	h5641	0.28746
h65432	0.253348	h56	0.016039	h564	0.279018
h563	0.248188	h6321	0.013046	h5	0.277279
h51	0.229491	h65412	0.008968	h65432 1	0.276785
h65431	0.225625	h632	0.002613	h65432	0.276236
h6321	0.220177	h421	-0.00267	h6413	0.258989
h5643	0.216146	h5642	-0.00499	h643	0.256949
h61432	0.213419	h42	-0.02174	h621	0.227481
h632	0.208917	h531	-0.02636	h5321	0.22426
h521	0.208236	h15432	-0.03263	h31	0.221367
h6432	0.205483	h61	-0.03941	h532	0.212599
h631	0.205297	h53	-0.04032	h62	0.209744
h1	0.197922	h5432	-0.04485	h3	0.207733
h63	0.191242	h6421	-0.04604	h65412	0.207681
h6413	0.185704	h5631	-0.05232	h5642	0.195692
h5	1.76E-01	h654321	-0.05748	h61432	0.193665
h643	0.173729	h563	-0.06709	h641	0.189785
h52	0.172072	h642	-0.07095	h6432	0.187531
h5421	0.168734	h6	-0.07156	h64	0.174333
h542	0.142555	h65432	-0.07201	h5431	0.173141
h541	0.138251	h4321	-0.07438	h1	0.172104
h54	0.107307	h31	-0.07815	h543	0.16075
h21	0.102132	h432	-0.09194	h321	0.116083
h421	0.093857	h541	-0.09239	h15432	0.111713
h41	0.060415	h631	-0.09778	h521	0.110939
h42	0.056061	h61432	-0.09896	h32	0.097008
h2	0.055946	h3	-0.09912	h5432	0.096483
h4	0.006869	h54	-0.11278	h431	0.08379
h15432	-0.00779	h63	-0.11834	h52	0.076149
h5321	-0.01189	h6432	-0.11948	h6421	0.075079
h5431	-0.03352	h5641	-0.12032	h43	0.063987
h5432	-0.03399	h5431	-0.12602	h541	0.055689
h532	-0.04172	h543	-0.14321	h642	0.046028
h531	-0.04426	h65431	-0.14388	h54	0.025193
h543	-0.06091	h564	-0.14409	h4321	0.011331
h53	-0.07824	h5643	-0.16295	h432	-0.0131
h4321	-0.08058	h431	-0.18699	h5421	-0.03584
h321	-0.09062	h6413	-0.19837	h542	-0.0704
h431	-0.11438	h41	-0.21387	h21	-0.08308
h432	-0.11629	h43	-0.21391	h2	-0.13378
h32	-0.12824	h641	-0.21545	h41	-0.14578
h31	-0.14143	h643	-0.22643	h4	-0.21951

h43	-0.15394	h64	-0.26576	h421	-0.22548
h3	-0.18989	h4	-0.26757	h42	-0.29042

388

389 **TABLE 4.** Proportion of all hypothesis including each of the six individual hypotheses significant at three
390 alpha levels (0.05, 0.1, and 0.2) for the spatial niche partitioning analysis.

Alpha Level	Hypothesis 6	Hypothesis 5	Hypothesis 4	Hypothesis 3	Hypothesis 2	Hypothesis 1
0.2	1	0.5	0.5	0	0.5	0.5
0.1	1	0.555556	0.111111	0	0.555556	0.444444
0.05	1	1	0	0	0.5	0

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393 **Table 5.** Proportion of all hypotheses including each of the six individual hypotheses significant at three
394 alpha levels (0.05, 0.1, and 0.2) for the combined spatial-temporal niche partitioning analysis.

Alpha Level	Hypothesis 6	Hypothesis 5	Hypothesis 4	Hypothesis 3	Hypothesis 2	Hypothesis 1
0.2	1	0.714286	0.142857	0.571429	0.285714	0.5
0.1	1	0.4	0	0.2	0	0.4
0.05	1	1	0	0	0	1

4. Discussion

4.1 Multi-model Evaluation of Hypotheses

Members of the felid guild in northern Myanmar partition their niches primarily in the spatial niche dimension, and to a lesser extent in time. We demonstrate strong support for hypothesis 6 in particular, and 5 and 6 together, in predicting the spatial partitioning and the joint space-time partitioning pattern among pairs of species. Hypothesis 6 proposed that there would be strong partitioning among golden cat and marbled cat, as the two guild members most similar in size, and there was universal support for significant niche partitioning among this pair of species. In contrast to our expectation, however, the partitioning between golden cat and marbled cat was most pronounced and statistically significant in the spatial dimension, and was not detected in the temporal dimension of niche overlap. We had expected large temporal displacement between these species based on published activity patterns, and that this might diminish the need for spatial displacement. On the contrary, we found relatively low temporal separation of the activity patterns of these species, but strong spatial partitioning.

Hypothesis 5 proposed there would be partitioning between clouded leopard and marbled cat, and that this again would be primarily in the temporal dimension. We found strong and significant partitioning between marbled cat and clouded leopard in the spatial dimension but, again, not in the temporal dimension.

The only other hypotheses to receive strong statistical support (significant at alpha 0.05) was hypothesis 2 for spatial overlap and hypothesis 1 for space-time joint niche overlap. Hypothesis 2 proposed that there would be similarly strong supported for spatial and joint space-time niche partitioning. Hypothesis 2 and 3 are similar in that they both postulate increasing displacement as pairs of species become increasingly similar in body size, with the difference being that in hypothesis 2 the difference is only between a focal species and tiger, while in hypothesis 1 it is between all pairs of species. The support for these hypotheses suggests that there is a general pattern of increasing displacement with decreasing difference in body size in the spatial dimension of the niche structure. The support for both hypothesis 1 and hypothesis 2 in the spatial and space-time overlap, respectively, suggests that tiger may indeed play a dominant role driving displacement of subordinate species (hypothesis 2), and that also there is a general pattern of larger spatial segregation among species of more similar body size. Collectively, these significant associations suggest that the main patterns of niche separation among the felid guild in northern Myanmar are spatial and not temporal. Further, they suggest that the largest separation is among species of similar body size, and in particular the dyads of golden cat-marbled cat and clouded leopard – marbled cat are the most highly divergent.

Interestingly we found little support in either the spatial and temporal dimensions of partitioning for hypothesis 4 and no support in the spatial dimension for hypothesis 3. These two hypotheses both propose partitioning between clouded leopard and both golden cat and marbled cat, with hypothesis 3 proposing this is in part driven by competitive release by tiger displacement of clouded leopard. Hypothesis 3 proposed meso-predator competitive release of golden cat and marbled cat resulting from displacement of clouded leopard by tiger. There was no support for this in the spatial dimension at any of the three alpha levels. In the joint spatial and temporal overlap, however, there was some support for hypothesis 3 (57% of models supported at 0.2 alpha level and 20% at 0.1, but 0 at 0.05). This suggests that there is no mesopredator competitive release of marbled cat and golden cat due to displacement of clouded leopards by tigers in space, but there may be displacement in time and space jointly that may reduce overlap of marbled cat and golden cat from clouded leopard, which may alleviate interference competition. Hypothesis 4 proposed displacement between clouded leopard and both golden cat and marbled cat independently of any associations with tiger. The weak support for these two hypotheses suggests overall there is not strong niche separation between clouded leopard and both golden cat and marbled cat (although see hypothesis 5 showing pairwise separation between clouded leopard and marbled cat), and that any displacement that exists cannot be explained by mesopredator release by displacement of clouded leopard by tiger.

Our results strongly suggested that the niches of the golden and marbled cats, two of the smaller felid species, exhibited the greatest niche displacement. The results may indicate that the larger cats all niche-pack to utilize the most abundant prey resources for species of middle to large size. In contrast, our results suggest that the marbled cat, being smaller and semi-arboreal (Sunquist & Sunquist, 2002), may be adapted to utilize a different prey base available in different space or time, or may be displaced, perhaps especially by golden cat, to suboptimal conditions providing lower resource availability. Furthermore, although the golden cat is closer to the marbled cat in weight, the slightly larger clouded leopard is closest to marbled cat in anatomy, so one cannot assume the potential for competition, or intra-guild hostility, is only determined by weight. Indeed, we found support for niche separation between marbled cat and clouded leopard, and not between clouded leopard and golden cat, suggesting other factors, such as morphology and behaviour, may affect this displacement in addition to body size alone.

We hypothesized that tiger presence reduces clouded leopard numbers and/or displaces them, thereby releasing the two smaller mesopredators, golden cats and marbled cats, from suppression by clouded leopards (Soule et al., 1988). We hypothesised that competitive release would apply to both golden cat and marbled cat if dominance by the tiger of the clouded leopards in turn reduced downward pressure on the other two. Our results suggest that the largest effect of competition on niche displacement may be between golden and marbled cats, and there is no evidence of competitive release. A plausible explanation may be that, given its smaller size and more agile anatomy, the marbled cat is better adapted to, and therefore retreats into, its own favoured realised niche, or that it is competitively displaced out of the niche space dominated by the golden cat and into a less optimal niche (Table 2).

Our results also showed that clouded leopard and golden cat had the highest total overlap, while clouded leopard and marbled cat had intermediate overlap. This does not suggest decisive

displacement of these two species by the dominant clouded leopard. Rather, it appears that there is partial displacement along different niche dimensions: clouded leopard overlapped less in space, but more in time, with golden cat than with marbled cat, and the clouded leopard/marbled cat dyad exhibited the greatest overlap in time, and least in space of any pairing. These partial displacements are further separated along the dimensions of weight and anatomy. Similar evidence of competitive displacement in a parallel, neotropical, felid guild was reported by Oliveira et al. (2010), who concluded that ocelots (*Leopardus pardalis*) affect the dynamics of smaller felids more strongly than did the largest member of the guild, the jaguar. However, based on the pattern of our multivariate hypothesis modeling we conclude that clouded leopard potential competition with marbled cat and golden cat is not extensive, whereas the golden cat and marbled cat are clearly the most segregated pairing.

Hearn et al. (2018) (see also Sunarto, Kelly, Parakkasi, & Hutajulu, 2015) reported that Sunda clouded leopards are nocturnal whereas marbled cats are diurnal, and so one of our hypotheses predicted that segregation on the temporal dimension would suffice to ameliorate competition, and therefore that the two species would not be displaced spatially. Our results do not strongly support this, with moderate overlap spatially (not unexpectedly large) and moderate temporal overlap (low but not statistically significant). This suggests that consistent with our expectation there is relatively low temporal overlap and somewhat higher spatial overlap between clouded leopard and marbled cat, but this is not a strong relationship.

In total these results suggest a complex pattern of guild assembly and potential competition leading to strong niche displacement between the golden cat and marbled cat, but high overlap between the relatively similarly-sized clouded leopard – golden cat, and the markedly differently-sized tiger – golden cat. This suggests that intraguild competition is not leading to behavioural displacement according to space or time between the species most likely to compete based on body size alone (clouded leopard and golden cat, clouded leopard and tiger). Rather, the salient displacement is between all three of the larger species and the smaller marbled cat. The marbled cat is anatomically, and in its patterned pelage, a diminutive replica of the clouded leopard, and Hearn et al. (2018) suggested that marbled cat may have a strong dietary preference for avian prey, while the other species are mostly predators of terrestrial quadrupeds. This might lead to substantial niche differentiation to optimize foraging.

Although we evaluated the individual and combined effects of multiple potential hypotheses of niche separation, and found support for some and no support for others, the observational and correlational nature of this study does not demonstrate causality. Therefore, future research using manipulative or comparative mensurative (McGarigal & Cushman, 2002) experiments should be undertaken to disentangle the multiple possible explanations of observed niche differentiation in the felid guild. The only way to reliably separate the multiple possible explanations of observed niche separation would be to implement experimental studies where some guild members are excluded (Krebs, 1991) or to conduct natural experiments replicated in multiple landscapes with different species combinations (Chiaverini et al., 2020). The observed patterns we saw, however, can exclude possible hypotheses (where displacement was not seen) and provide support for the possibility of others (where displacement was seen consistent with expectations). Given the difficulty of conducting controlled

experiments and species exclusion studies on endangered and rare carnivores, experimental studies are unlikely. However, meta-replicated studies repeating niche overlap analysis across the ranges of these species and in multiple locations where different combinations of species are present are plausible and would enable more definitive inference about the potential drivers of observed niche separation among these members of the felid guild.

4.2 Conservation Implications

The HWS was selectively logged for timber during the decade prior to our study. The high relative space use by clouded leopard suggests that it may be more tolerant of habitat modification associated with human disturbance and potential exploitation than is the tiger. This is broadly consistent with previous reports of clouded leopards occurring in secondary forest (Hearn et al., 2018). However, in contrast to these previous studies, we found no evidence of clouded leopard selectively using forest edges (e.g., Rabinowitz et al., 1987; Hunter, 2015 and, for the Sunda species Haidir et al., 2018, Hearn et al. 2018). Proximity to the main streams had little effect on predicted space use of any of the species in our model; however, we note the lack of tiger tracks and signs near the main river in the north-eastern section of the study area, which was heavily frequented by gold miners and trespassing boats. These observations accord with the conclusions of Naing et al. (2019) who drew attention to the greater abundance of felids in the less threatened zones of the park. Tigers are well-known to adapt to human disturbance, where they are not directly persecuted (Carter et al., 2012, 2015; Naha et al., 2016). Our field observations may suggest active persecution of tigers, likely in the form of elevated poaching, in areas where human activity was highest. The lack of observed avoidance of these areas by the other felid species suggests they may be less vulnerable to human disturbance or poaching than are tigers.

Human disturbance, as detected on our cameras, was very frequent on the former logging roads connecting the western and eastern parts of the sanctuary, and all five species, most especially clouded leopards, were positively associated with these areas, and thus human detections, suggesting no avoidance of human activity and active selection of roads and trails due to their facilitation of movement (e.g., Hearn et al., 2018). Similarly, male Sunda clouded leopards have been found to preferentially travel roads and trails in Sabah, Borneo (Hearn et al., 2018) and also in Kalimantan, Borneo (Gordon & Stewart, 2007). However, this shared use of trails by humans and felids may come at the cost of increased poaching risk.

4.3 Scope and Limitations

Camera trapping data provide powerful, but limited, insight into species niches. The locations and times at which the different species are detected across our large and long-term survey provide valuable insight into overlap in space and time of these species. However, the data are limited to detections at the location of the camera traps, and thus do not reflect the full spatial and temporal activity pattern of any of the focal species. Also, we designed our surveys targeting larger carnivores thus it may affect comparisons of estimations among them. However, it is also not possible to simultaneously design a survey for all species and we had to choose the largest extent for covariates in space use estimations. GPS telemetry on multiple individuals of each of the species in the same study region would provide a valuable comparison from a dataset that provides much higher precision of

temporal and spatial activity and also provides measures of space-time avoidance of guild members which camera data cannot provide.

While camera trapping provides only snapshots, our study benefitted from the amalgamation of several data sets providing coverage across an unusually large extent in both space and time, which improves the clarity of our conclusions. We also faced the likelihood of low detection probabilities in the dense forest of HMS, and the unknown proportion of arboreal activity amongst the species (Haidir et al., 2018), and equally unknown detail of their prey species (or age). We excluded some data while standardizing the analysis of space use, but we maximised the inclusion of data for diel activity analysis which enables us to check the representativeness of species' detection and activity. The almost identical activity pattern revealed that using two datasets with different sample sizes provided confidence in our interpretation of temporal and, albeit to a lesser extent, spatial overlap. Our survey also provided the comparable findings for temporal activity of felids in the region locally (Zaw et al., 2014) and others (Table S7).

We focused on interactions among five co-occurring felid species given the expected strong interactions among them due to taxonomic and anatomical similarity. However, there are other species in this ecosystem that may affect the habitat use and temporal activity of these felid species through intimidation, kleptoparasitism, competitive exclusion and mortality (Palomares & Caro, 1999; Vanak et al., 2013). For example, presence of dholes (*Cuon alpinus*) and Malayan sun bears (*Helarctos malayanus*) may affect all the studied species individually and interact to drive the process of mesopredator release in HWS. Dholes might be direct competitors for food with any of the felids (Thinley et al., 2011), with observations suggesting this for at least tiger and clouded leopard (e.g., Singh, Srivathsa, & Macdonald, 2019). By analogy, there are documented instances where a pack of dholes tree a leopard and even drive a tiger away from its kills (Karanth & Sunquist, 2000; Venkataraman, 2017). In addition, dholes and bears, while not necessarily competing for food with Asiatic golden cat and marbled cat, might have antagonistic interactions that affect space and temporal use of the smaller cat species. For example, leopard may kill sun bear cubs (Naing et al., 2020). In a complex multi-species trophic community, mesopredator release might be affected by the presence of species dominant to them but subordinate to the apex species. Therefore, this study takes advantage of the strong morphological similarities between the five felids, simplifying the focus of competition between them, while mindful of the wider network of interacting species and even more complex trophic interactions amongst the wider community of predators. Future work should face the considerable challenge of incorporating more carnivore species into such analyses of niche interaction and displacement.

The largest challenge our study faced in terms of providing clear explanation of observed relationships is the fact that observational studies in single systems cannot reliably separate the multiple potential explanations of observed patterns (e.g., McGarigal & Cushman, 2002). This is particularly the case in community ecology studies attempting to quantify effects of competition on niche separation (Connell, 1980). We found complex patterns of niche overlap and partial separation among five felid guild members that suggest varying degrees of niche differentiation; we cannot confirm the causes of these differences. Experimental studies that either manipulatively (Krebs, 1991) or mensuratively (Chiaverini et al., 2020) control species co-occurrence patterns are needed to reliably infer effects of

589 current competition on niche structure and to separate it from evolutionary differences in adapted niche
590 structure resulting, in part, from past competition in the evolutionary history of the species (Connell,
591 1980). Thus, we strongly suggest future work with meta-replicated studies that provide multiple
592 sampled landscapes with different species combinations, given the impossibility of manipulative species
593 exclusion experiments for threatened and endangered species, such as felids in Southeast Asia.

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Conflicts of Interests

None declared.

Author Contribution

PPK, DWM, HN and SH conceived and designed the project. PPK and HN collected and compiled the data. Data analysis was done by PPK, UP and SC. PPK, DWM, DB, UP, SH, HN, DB, ZK and SC wrote the manuscript.

Data Accessibility

Additional supporting results are reported with supporting information. The species detection data contain geographic locations of Endangered (tiger) and Vulnerable (clouded leopard) species and will not be made publicly available. However, request can be made to the corresponding author to gain access for academic purpose.

References

- Arino, O., Ramos Perez, Jose Julio Kalogirou, V., Bontemps, S., Defourny, P., & Van Bogaert, E. (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*. © European Space Agency (ESA) & Université Catholique de Louvain. <https://doi.org/10.1594/PANGAEA.787668>
- Ash, E., Cushman, S. A., Macdonald, D. W., Redford, T., & Kaszta, Ž. (2020). How important are resistance, dispersal ability, population density and mortality in temporally dynamic simulations of population connectivity? A case study of tigers in Southeast Asia. *Land*, 9(11), 1–27. <https://doi.org/10.3390/land9110415>
- Ash, E., Hallam, C., Chanteap, P., Kaszta, Ž., Macdonald, D. W., Rojanachinda, W., Redford, T., & Harihar, A. (2020). Estimating the density of a globally important tiger (*Panthera tigris*) population: Using simulations to evaluate survey design in Eastern Thailand. *Biological Conservation*, 241(October 2019), 108349. <https://doi.org/10.1016/j.biocon.2019.108349>
- Bischof, R., Ali, H., Kabir, M., Hameed, S., & Nawaz, M. A. (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology*, 293(1), 40–48. <https://doi.org/10.1111/jzo.12100>
- Blonder, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, 41(9), 1441–1455. <https://doi.org/10.1111/ecog.03187>
- BRSoftware. (2012). *BR's EXIFextracter* (0.9.10 beta). <https://www.br-software.com/extracter.html>
- Can, Ö. E., Yadav, B. P., Johnson, P. J., Ross, J., D'Cruze, N., & Macdonald, D. W. (2020). Factors affecting the occurrence and activity of clouded leopards, common leopards and leopard cats in the Himalayas. *Biodiversity and Conservation*, 29, 839–851. <https://doi.org/10.1007/s10531-019-01912-7>
- Caro, T. (2007). Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution*, 22(8), 394–400. <https://doi.org/10.1016/j.tree.2007.06.003>
- Carter, N. H., Jasny, M., Gurung, B., & Liu, J. (2015). Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation*, 3, 149–162. <https://doi.org/10.1016/j.gecco.2014.11.013>
- Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the United States of America*, 109(38), 15360–15365. <https://doi.org/10.1073/pnas.1210490109>
- Cheyne, S. M., & MacDonald, D. W. (2011). Wild felid diversity and activity patterns in Sabangau peat-swamp forest, Indonesian Borneo. *Oryx*, 45(1), 119–124. <https://doi.org/10.1017/S003060531000133X>
- Chiaverini, L., Macdonald, D. W., Hearn, A. J., Cheyne, S. M., Haidir, I. A., Hunter, L. T. B., Kaszta, Z., Linkie, M., Macdonald, E. A., Ross, J., Wan, H. Y., & Cushman, S. A. (2020). *Hostility and tyranny in the uneasy coexistence in guilds of Sunda Islands felids, from tigers to leopard cats*. Manuscript in preparation.
- Connell, J. H. (1980). Diversity and the coevolution of competitors , or the ghost of competition past. *Oikos*, 35(2), 131–138. <https://www.jstor.org/stable/3544421>

- 659 Crooks, K. ., & Soule, M. . (1999). Mesopredator release and avifaunal extinctions in a fragmented
660 system. *Nature*, 400(5), 563–566.
- 661 Cushman, S. A., McKelvey, K. S., Hayden, J., & Schwartz, M. K. (2006). Gene flow in complex landscapes:
662 Testing multiple hypotheses with causal modeling. *American Naturalist*, 168(4), 486–499.
663 <https://doi.org/10.1086/506976>
- 664 Davey, K., Wachter, T., & Amin, R. (2015). *Analysis tool for camera trap survey data*, ZSL (in. Prep).
- 665 Dayan, T., Simberloff, D., & Yom-tov, Y. (1989). Inter- and intraspecific character displacement in
666 mustelids. *Ecological Research*, 70(5), 1526–1539. <https://doi.org/10.2307/1938210>
- 667 Estes, J. A. (1996). Predators and ecosystem management. *Wildlife Society Bulletin*, 24(3), 390–396.
668 www.jstor.org/stable/3783318
- 669 Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data*
670 *analysis* (3rd ed.). Chapman and Hall/CRC.
- 671 Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences.
672 *Statistical Science*, 7(4), 457–472. https://projecteuclid.org/download/pdf_1/euclid.ss/1177011136
- 673 Gordon, C. H., & Stewart, A. E. (2007). The use of logging roads by clouded leopard. *Cat News*, 47, 12–
674 13.
- 675 Haidir, I. A., Dinata, Y., Linkie, M., & Macdonald, D. W. (2013). Asiatic golden cat and Sunda clouded
676 leopard occupancy in the Kerinci Seblat landscape, West-Central Sumatra. *CatNews*, 59, 2013.
- 677 Haidir, I. A., Macdonald, D. W., & Linkie, M. (2018). Assessing the spatiotemporal interactions of
678 mesopredators in Sumatra's tropical rainforest. *PLOS ONE*, 13(9), e0202876.
679 <https://doi.org/10.1371/journal.pone.0202876>
- 680 Hearn, A. J., Cushman, S. A., Ross, J., Goossens, B., Hunter, L. T. B., & Macdonald, D. W. (2018). Spatio-
681 temporal ecology of sympatric felids on Borneo. Evidence for resource partitioning? *PLoS ONE*,
682 13(7), e-0200828. <https://doi.org/10.1371/journal.pone.0200828>
- 683 Hegel, T. M., Myserud, A., Huettmann, F., & Stenseth, N. C. (2010). Interacting effect of wolves and
684 climate on recruitment in a northern mountain caribou population. *Oikos*, 119(9), 1453–1461.
685 <https://doi.org/10.1111/j.1600-0706.2010.18358.x>
- 686 Hunter, L. (2015). *Wild cats of the world* (1st ed.). Bloomsbury.
- 687 Hutchinson, G. E. (1957). Concluding remarks. Population studies: animal ecology and demography. *Cold*
688 *Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.
689 <https://doi.org/doi:10.1101/sqb.1957.022.01.039>
- 690 Karanth, K. U., & Sunquist, M. E. (2000). Behavioural correlates of predation by tiger (*Panthera tigris*),
691 leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology*,
692 250(2), 255–265. <https://doi.org/10.1017/S0952836900002119>
- 693 Kaszta, Ż., Cushman, S. A., & Macdonald, D. W. (2020). Prioritizing habitat core areas and corridors for a
694 large carnivore across its range. *Animal Conservation*, (In press).
695 <https://doi.org/10.1111/acv.12575>
- 696 Krebs, C. J. (1991). The experimental paradigm and long-term population studies. *International Journal*

697 of *Avian Science*, 133(S1), 3–8. <https://doi.org/10.1111/j.1474-919X.1991.tb07663.x>

698 Legendre, P., & Legendre, L. (1998). *Numerical Ecology*. Elsevier.

699 Linkie, M., & Ridout, M. (2011). Assessing tiger-prey interactions in Sumatran rainforests. *Journal of*
700 *Zoology*, 284(3), 224–229. <https://doi.org/10.1111/j.1469-7998.2011.00801.x>

701 Lynam, A. J., Jenks, K. E., Steinmetz, R., & Reed, D. H. (2013). Terrestrial activity patterns of wild cats
702 from camera-trapping. *The Raffles Bulletin of Zoology*, 61(1), 407–415.
703 <https://lkc.nhm.nus.edu.sg/app/uploads/2017/06/61rbz407-415.pdf>

704 Macdonald, D. W., Bothwell, H. M., Kaszta, Z., Ash, E., Bolongon, G., Burnham, D., Can, Ö. E., Campos –
705 Arceiz, A., Channa, P., Clements, G. R., Hearn, A. J., Hedges, L., Htun, S., Kamler, J. F., Kawanishi, K.,
706 Macdonald, E. A., Mohamad, S. W., Moore, J., Naing, H., ... Cushman, S. A. (2019). Multi-scale
707 habitat modelling identifies spatial conservation priorities for mainland clouded leopards (*Neofelis*
708 *nebulosa*). *Diversity and Distributions*, 25(10), 1–16. <https://doi.org/10.1111/ddi.12967>

709 Macdonald, D. W., & Loveridge, A. J. (2010). *Biology and conservation of wild Felids*. Oxford University
710 Press.

711 Macdonald, D. W., Loveridge, A. J., & Nowell, K. (2010). Dramatis personae: an introduction to the wild
712 felids. In D. W. Macdonald & A. J. Loveridge (Eds.), *The Biodiversity and Conservation of Wild Felids*
713 (pp. 3–58). Oxford University Press.

714 Macdonald, D. W., Newman, C., & Harrington, L. A. (2017). *Biology and conservation of musteloids*.
715 Oxford University Press.

716 Macdonald, D. W., & Sillero-zubiri, C. (2004). *The biology and conservation of wild Canids*. Oxford
717 University Press.

718 Mackenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site
719 occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*,
720 84(8), 2200–2207.

721 MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002).
722 Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8),
723 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

724 MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). *Occupancy*
725 *estimation and modeling: Inferring patterns and dynamics of species occurrence* (2nd ed.).
726 Academic Press.

727 Mantel, N. (1967). The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer*
728 *Research*, 27(2), 209–220.

729 Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple
730 scales. *Ecoscience*, 16(2), 238–247. <https://doi.org/10.2980/16-2-3238>

731 McGarigal, K., & Cushman, S. A. (2002). Comparative evaluation of experimental approaches to the
732 study of habitat fragmentation effects. *Ecological Applications*, 12(2), 335–345.
733 <https://doi.org/10.2307/3060945>

734 Meredith, M., & Ridout, M. S. (2017). Overview of the overlap package. *R Project*, 1–9.
735 <http://cran.radicaldevelop.com/web/packages/overlap/vignettes/overlap.pdf>

736 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity
737 hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>

738 Naha, D., Jhala, Y. V., Qureshi, Q., Roy, M., Sankar, K., & Gopal, R. (2016). Ranging, activity and habitat
739 use by tigers in the mangrove forests of the Sundarban. *PLoS ONE*, 11(4), e0152119.
740 <https://doi.org/10.1371/journal.pone.0152119>

741 Naing, H., Htun, S., Kamler, J. F., Burnham, D., & Macdonald, D. W. (2020). *Large carnivores as potential*
742 *predators of sun bears*. *January*. <https://doi.org/10.2192/URSU-D-18-0022.2>

743 Naing, H., Ross, J., Burnham, D., Htun, S., & Macdonald, D. W. (2019). Population density estimates and
744 conservation concern for clouded leopards *Neofelis nebulosa*, marbled cats *Pardofelis marmorata*
745 and tigers *Panthera tigris* in Htamanthi Wildlife Sanctuary, Sagaing, Myanmar. *Oryx*, 53(4), 654–
746 662. <https://doi.org/10.1017/s0030605317001260>

747 Northrup, J. M., & Gerber, B. D. (2018). A comment on priors for Bayesian occupancy models. *PLoS ONE*,
748 13(2), 1–13. <https://doi.org/10.1371/journal.pone.0192819>

749 Odden, M., Wegge, P., & Fredriksen, T. (2010). Do tigers displace leopards? If so, why? *Ecological*
750 *Research*, 25(4), 875–881. <https://doi.org/10.1007/s11284-010-0723-1>

751 Oliveira, T. G. De, Tortato, M. A., Silveira, L., Kasper, B. C., Mazim, F. D., Lucherini, M., Jacomo, A. T.,
752 Soares, J. B. G., Marques, R. V., & Sunquist, M. (2010). Ocelot ecology and its effect on the small-
753 felid guild in the lowland neotropics. In D. W. MacDonald & A. J. Loveridge (Eds.), *Biology and*
754 *conservation of wild Felids* (pp. 559–580). Oxford University Press.

755 Olliff, E. R. R., Cline, C. W., Bruen, D. C., Yarmchuk, E. J., Pickles, R. S. A., & Hunter, L. (2013). The
756 Panthercam-a camera-trap optimized for monitoring wild felids. *The Wild Felid Monitor*, 7(2), 21–
757 28.

758 Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American*
759 *Naturalist*, 153(5), 492–508. <https://doi.org/10.1086/303189>

760 PantheraCameraTrap. (2012). *Camera trap file manager* (1.9.6). <http://pantheracameratrap.org>

761 Penjor, U., Macdonald, D. W., Wangchuk, S., Tandin, T., & Tan, C. K. W. (2018). Identifying important
762 conservation areas for the clouded leopard *Neofelis nebulosa* in a mountainous landscape:
763 Inference from spatial modeling techniques. *Ecology and Evolution*, 8(8), 4278–4291.
764 <https://doi.org/10.1002/ece3.3970>

765 Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
766 *Proceedings of the 3rd International Conference on Distributed Statistical Computing*, 1–10. [http://](http://www.ci.tuwien.ac.at/Conferences/DSC-2003/)
767 www.ci.tuwien.ac.at/Conferences/DSC-2003/

768 R Core Team. (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for
769 Statistical Computing. <http://www.r-project.org/>

770 Rabinowitz, A., Andau, P., & Chai, P. P. K. (1987). The clouded leopard in Malaysian Borneo. *Oryx*, 21(2),
771 107–111. <https://doi.org/10.1017/s0030605300026648>

772 Rabinowitz, A., Schaller, G. B., & Uga, U. (1995). A survey to assess the status of Sumatran rhinoceros
773 and other large mammal species in Tamanthi Wildlife Sanctuary, Myanmar. *Oryx*, 29(2), 123–128.
774 <https://doi.org/10.1017/S0030605300020998>

- 775 Rasphone, A., Kery, M., Kamler, J. F., & Macdonald, D. W. (2019). Documenting the demise of tiger and
776 leopard , and the status of other carnivores and prey , in Lao PDR ' s most prized protected area :
777 Nam Et - Phou Louey. *Global Ecology and Conservation*, 20(20), 1–15.
778 <https://doi.org/10.1016/j.gecco.2019.e00766>
- 779 Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data.
780 *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337.
- 781 Singh, P., & Macdonald, D. W. (2017). Populations and activity patterns of clouded leopards and marbled
782 cats in Dampa Tiger Reserve, India. *Journal of Mammalogy*, 98(5), 1453–1462.
783 <https://doi.org/10.1093/jmammal/gyx104>
- 784 Singh, P., Srivathsa, A., & MacDonald, D. W. (2019). Conservation status of the dhole *Cuon alpinus* in
785 north-east India, with a focus on Dampa Tiger Reserve, Mizoram. *Oryx*, 1–5.
786 <https://doi.org/10.1017/S0030605319000255>
- 787 Soule, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M., & Hill, S. (1988). Reconstructed dynamics
788 of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology*, 2(1),
789 75–92. <http://www.jstor.org/stable/2386274>
- 790 Su, Y.-S., & Yajima, M. (2015). *R2jags: Using R to run "JAGS."* <https://cran.r-project.org/package=R2jags>
- 791 Sunquist, M., & Sunquist, F. (2002). Marbled cat *Pardofelis marmorata*(Martin 1837). In *Wild cats of the*
792 *world* (pp. 373–376). The University of Chicago Press.
- 793 Tan, C. K. W., Rocha, D. G., Reuben, G., Brenes-mora, E., Hedges, L., Kawanishi, K., Wan, S., Rayan, D. M.,
794 Bolongon, G., Moore, J., Wadey, J., Campos-arceiz, A., & Macdonald, D. W. (2017). Habitat use and
795 predicted range for the mainland clouded leopard *Neofelis nebulosa* in Peninsular Malaysia.
796 *Biological Conservation*, 206, 65–74. <https://doi.org/10.1016/j.biocon.2016.12.012>
- 797 Thinley, P., Kamler, J., Wang, S. W., Lham, K., Stenkewitz, U., & Macdonald, D. W. (2011). Seasonal diet
798 of dholes (*Cuon alpinus*) in northwestern Bhutan. *Mammalian Biology*, 76(4), 518–520.
799 <https://doi.org/10.1016/j.mambio.2011.02.003>
- 800 Vanak, A. T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R. (2013). Moving to
801 stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology*, 94(11),
802 2619–2631. <https://doi.org/10.1890/13-0217.1>
- 803 Venkataraman, A. B. (2017). *Do dholes (Cuon alpinus) live in packs in response to competition with or*
804 *predation by large cats ? Arun B . Venkataraman Published by : Current Science Association Stable*
805 *URL : <http://www.jstor.org/stable/24097>. 69(11), 934–936.*
- 806 Waddle, J. H., Dorazio, R. M., Walls, S. C., Rice, K. G., Schuman, M. J., Mazzotti, F. J., Waddle, J. H.,
807 Dorazio, R. M., Walls, S. C., Rice, K. G., Beauchamp, J., Schuman, M. J., & Mazzotti, F. J. (2010). *A*
808 *new parameterization for estimating co-occurrence of interacting species.* 20(5), 1467–1475.
809 <http://www.jstor.org/stable/25680391>
- 810 Wand, M. P., & Jones, M. C. (1994). *Kernal smoothing* (1st ed.). Chapman and Hall/CRC. <https://doi.org/>
811 <https://doi.org/10.1201/b148766>
- 812 Zaw, T., Myint, T., Htun, S., Po, S. H. T., Latt, K. T., Maung, M., & Lynam, A. J. (2014). Status and
813 distribution of smaller cats in Myanmar. *Cat News*, 8, 24–30.

814

815

816