

TERRESTRIAL ACTIVITY PATTERNS OF WILD CATS FROM CAMERA-TRAPPING

Antony J. Lynam

Wildlife Conservation Society, Global Conservation Program, 2300 Southern Boulevard, Bronx, NY, 10540, USA
Email: tlynam@wcs.org

Kate E. Jenks

Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, 03824, USA
Graduate Programs in Organismic and Evolutionary Biology, and Wildlife and Fisheries Conservation, University of Massachusetts
611 N. Pleasant Street, Amherst, MA, 01003, USA
Smithsonian Conservation Biology Institute, Smithsonian National Zoological Park
1500 Remount Road, Front Royal, VA, 22630, USA
Email: kate@katejenks.info

Naruemon Tantipisanuh, Wanlop Chutipong, Dusit Ngoprasert and George A. Gale

Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Bangkok, 10150, Thailand
Email: ttpisanu@gmail.com (NT), wanlop.chutipong2012@gmail.com (WC), ndusit@gmail.com (DN), ggkk1990@gmail.com (GG)

Robert Steinmetz

WWF Thailand, Ladayao, Jatujak, Bangkok, Thailand
Email: roberts@wwfgreatermekong.org

Ronglarp Sukmasuang and Naris Bhumpakphan

Department of Forest Biology, Kasetsart University, Bangkok 10900, Thailand
Email: fforrls@ku.ac.th (RS), fforrnrb@ku.ac.th (NB)

Lon I. Grassman, Jr.

Feline Research Center, Caesar Kleberg Wildlife Research Institute, MSC 218, 700 University Blvd.
Texas A&M University-Kingsville, Kingsville, TX, 78363, USA
Email: longrassman@hotmail.com

Passanan Cutter

Conservation Biology Program, University of Minnesota, 187 McNeal Hall, 1985 Buford Avenue, St. Paul, MN, 55108, USA
Email: namfonb@yahoo.com

Shumpei Kitamura

Division of Nature and Environmental Management, The Museum of Nature and Human Activities
Hyogo, Yayoigaoka 6, Sanda, 669-1546, Japan
Email: kshumpei@wg8.so-net.ne.jp

David H. Reed

Department of Biology, University of Louisville, Louisville, KY, 40292, USA

Megan C. Baker, William McShea, Nucharin Songsasen, and Peter Leimgruber
Smithsonian Conservation Biology Institute, Smithsonian National Zoological Park
1500 Remount Road, Front Royal, VA, 22630, USA
Email: bakermc@si.edu (MB), bakermc@si.edu (WM), songsasenn@si.edu (NS), leimgruber@si.edu (PL)

ABSTRACT. — The behaviour of wild cats is poorly understood. Using camera-trapping, we quantified temporal overlap among seven species of Asian wild cats, including tiger *Panthera tigris* and leopard *Panthera pardus*. Based on time stamp data from 780 camera-traps and 24 study sites from 14 protected areas across Thailand, we assessed terrestrial activity patterns and temporal overlap in habitat use. For quantifying overlap, we used a coefficient estimator $\hat{\Delta}_1$ that allows for calculation of confidence intervals. Our study provided insight into temporal interactions among species of wild cats, particularly between small cats and their larger cat relatives. We found temporal habitat segregation in several small cats with some species being strongly nocturnal ($\geq 85\%$ records between 1800 and 0600 hours – leopard cat *Prionailurus bengalensis*), mostly ($> 50\%$) nocturnal (clouded leopard *Neofelis nebulosa*), mostly diurnal ($> 50\%$ records between 0600 and 1800 hours – Asiatic golden cat *Catopuma temminckii*), or strongly ($\geq 85\%$) diurnal (marbled cat *Pardofelis*

marmorata). We found high temporal overlap ($\hat{A}_1 \geq 0.80$) between leopard cat and clouded leopard (95% CI = 0.77–0.91), Asiatic golden cat and leopard (95% CI = 0.69–0.87), Asiatic golden cat and tiger (95% CI = 0.72–0.90), and clouded leopard and tiger (95% CI = 0.69–0.85). Our research demonstrates that temporal habitat or niche segregation may be an important process in maintaining the functioning of diverse predator guilds in tropical forests. We developed several avoidance or overlap hypotheses that can explain the patterns observed in our study and that should be further tested.

KEY WORDS. — small cats, activity patterns, camera-traps, Thailand

INTRODUCTION

The ecology particularly of wild cats is poorly known. With the exception of a few studies (Rabinowitz, 1989, 1991; Grassman, 2000; Grassman et al., 2005a; Rajaratnam et al., 2007; Baker et al., 2011), we know relatively little of the interactions among species within the felid guild (Tantipisanuh et al., in press).

Camera-trapping has improved our ability to study activity and terrestrial movements of Asian tropical forest fauna that are difficult to see or are rare (van Schaik & Griffiths, 1996), species diversity (Kitamura et al., 2010), the associations among species (Ngoprasert et al., 2012), and their habitats (Gray & Phan, 2012). Time stamps recorded in photographs provide a detailed account of species activity patterns (Laidlaw & Shaharuddin, 1998; Kawanishi & Sunquist, 2004). Such data can be used to study processes shaping ecological communities, especially whether potentially competing species overlap or avoid each other temporally, and how larger species might influence activity of their smaller cohorts in the same habitat. There are numerous studies about coexistence and resource partitioning between predators in tropical forests (e.g., Terborgh, 1992; Karanth & Sunquist, 1995; Ray & Sunquist, 2001; Scognamillo et al., 2003; Steinmetz et al., in press), but few focus on temporal patterns of habitat use.

In this study we measured terrestrial activity patterns for five small cats using a broad-scale data set from 24 sites across 14 Thailand protected areas, and quantify temporal overlap in habitat use among smaller cats and their larger relatives (i.e., leopard and tiger), and between the larger cats. We discuss observed patterns of overlap in the context of what is known about feeding ecology and habitat preference of the individual species.

MATERIAL AND METHODS

Study area. — Thailand (513,115 km²) spans latitudes 5°37'N to 20°30'N and ranges in elevation from sea level to 2,565 m. The country has 123 national parks (60,320 km²), 58 wildlife sanctuaries (36,929 km²), and 60 non-hunting areas (5,233 km²; DNP, 2010). Logging concessions were revoked country-wide in 1989 and since then there has been no legal logging of natural forests. As of 2010, 13% of the country

was classified as primary forest (FAO, 2010). The main forest types include deciduous forests (mixed and dry dipterocarp) found in drier areas (<1,500 mm rain), and evergreen forests (rainforest, monsoon, and dry evergreen) found in wetter areas (>1,500 mm rain). Camera-trap capture time and species data were available from 24 separate studies (Tantipisanuh et al., in press) across 14 protected areas, stratified across these forest types (Fig. 1; Table 1).

Camera-trap data collection. — The 24 studies had varying objectives. One study at Halabala Wildlife Sanctuary was undertaken to sample overall diversity of mammals (Kitamura et al., 2010). Three studies at Khao Sok, Khao Sam Roi Yod and Thale Noi were done specifically to collect ecological information on fishing cats (*Prionailurus viverrinus*; Cutter & Cutter, 2009). For 20 other studies (83%), the objective was to collect information on large cats, especially tigers, and other large mammals, so records of small cats were incidental.

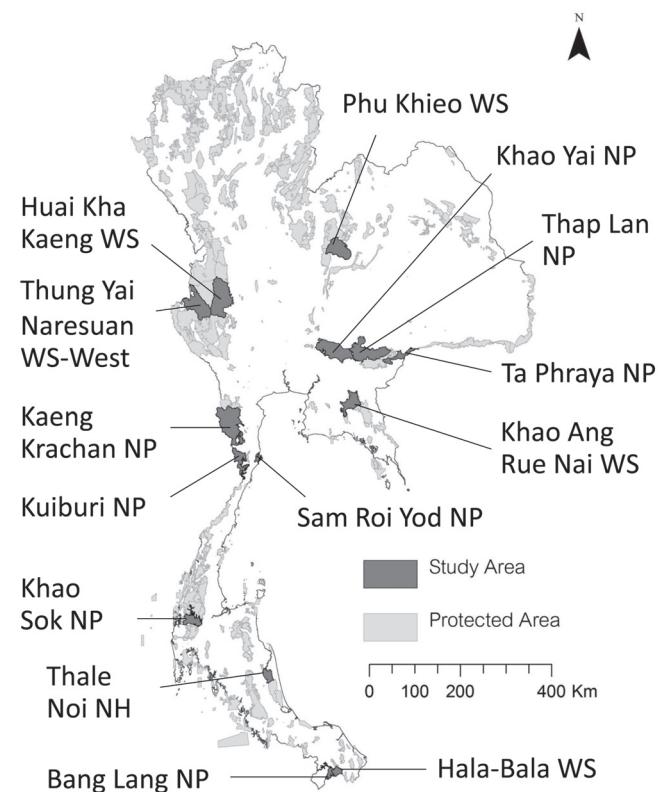


Fig. 1. Camera trap data was collected from 14 protected areas within Thailand. NP = national park; WS = wildlife sanctuary; NH = non-hunting area.

Table 1. Number of photographs with time/date stamp data of wild cats from 14 protected areas in Thailand.

	Leopard cat	Fishing cat	Asiatic golden cat	Marbled cat	Clouded leopard	Leopard	Tiger
Bang Lang NP	0	0	0	0	4	0	17
Hala-Bala WS	12	0	42	1	7	2	13
Huai Kha Kaeng WS	61	0	3	1	3	145	92
Kaeng Krachan NP	37	1	2	1	0	174	21
Khao Ang Rue Nai WS	32	0	1	1	9	0	0
Khao Sam Roi Yod NP	0	4	0	0	0	0	0
Khao Sok NP	2	0	0	0	0	0	0
Khao Yai NP	51	0	13	4	37	0	6
Kuiburi NP	23	0	14	2	1	65	19
Phu Khieo WS	9	0	3	0	6	0	6
Ta Phraya NP	13	0	0	0	11	2	0
Thale Noi NH	0	1	0	0	0	0	0
Thap Lan NP	0	0	1	0	0	0	0
ThungYai -West WS	18	0	2	0	1	14	24
Total	258	6	81	10	79	402	198

NP = National Park; WS = Wildlife Sanctuary; NH = Non-hunting Area

However, across sites, camera-traps were consistently placed along animal trails following ridges and water crossings. Due to use of a range of different camera-trap models, during the days some camera-trap models using heat in motion sensors might perform less reliably than during the cooler nights. At all sites except for Khao Sam Roi Yod, where sampling was stopped during daylight hours due to security concerns, cameras were set to record activity 24 h per day. Therefore, while detection probabilities for small cats were not optimised at every site, at all but Khao Sam Roi Yod there should have been no temporal bias in the probability of being detected.

Photographs were independently verified before inclusion in the dataset (Tantipisanuh et al., in press). Photographs with time/date stamps were obtained from camera-traps for leopard cat, fishing cat, Asiatic golden cat, marbled cat, clouded leopard, leopard, and tiger across the study areas from 1996 until 2011 (Table 1). Individual camera-trap placement and details of camera-trapping including species present, data and year of survey, survey effort, camera Universal Transverse Mercator locations, habitat, and elevation are reported in Ngoprasert et al. (2012). For each species data were pooled and we defined activity pattern as day-time for photographs of cats obtained during 0601–1759 hours and night-time for those taken during 1800–0600 hours (Azlan & Sharma, 2006; Azlan et al., 2009). We defined activity as strongly nocturnal ($\geq 85\%$ of observations between 1800–0600 hours), mostly nocturnal (61–84% of observations between 0600–1800 hours), cathemeral (40–60% of activity during day or night), mostly diurnal (61–84% of observations between 0600–1800 hours), or strongly diurnal ($\geq 85\%$ of observations between 0600–1800 hours). The categories were established as a way of refining previous more simplistic classifications of activity pattern (van Schaik & Griffiths, 1996).

Activity analysis. — As some cat species may be partly arboreal, and since our camera-traps only recorded activity at ground-level, we were unable to assess arboreal activity. Capture times for each species were regarded as a random sample of photographs taken at any time of the day. We estimated the daily activity pattern overlap between sympatric cat species by applying the statistical methodology developed by Ridout & Linkie (2009). We computed each species' terrestrial activity pattern separately using kernel density estimation or by fitting trigonometric sum distributions (Fernandez-Duran, 2004). Then, a measure of overlap between two focal species' distributions was calculated. Ridout & Linkie (2009) favoured the coefficient of overlapping, Δ , which is defined as the area under the curve that is formed by taking the minimum of the two density functions at each time point. The coefficient of overlap = 1 if the activity densities are identical and = 0 if they have no common active period.

We obtained confidence intervals as percentile intervals from 500 bootstrap samples. All statistics were performed in R version 2.11.1 (R Development Core Team, 2009) following the code made available by Linkie & Ridout (2011). We used the $\hat{\Delta}_1$ estimator for the coefficient of overlap because it is recommended for small sample sizes (Ridout & Linkie, 2009). $\hat{\Delta}_1$ is a label consistent with discussions in Ridout & Linkie (2009) and is defined as:

$$\hat{\Delta}_1 = \int_0^1 \min \{ \hat{f}(t), \hat{g}(t) \} dt$$

RESULTS

Seven felids were recorded using camera-traps across 14 protected areas (Table 1). Fishing cat ($n = 6$) and marbled cat ($n = 10$) had the fewest detections. In none of the study

Table 2. Estimates of activity pattern overlap ($\hat{\Delta}_1$) between felid species (1 = identical activity), with approximate 95% bootstrap confidence intervals in parentheses.

	Asiatic golden cat	Marbled cat	Clouded leopard	Leopard	Tiger
Leopard cat	0.63 (0.52–0.71)	0.31 (0.16–0.39)	0.90 (0.77–0.91)	0.50 (0.44–0.56)	0.73 (0.65–0.79)
Asiatic golden cat		0.61 (0.30–0.68)	0.72 (0.58–0.81)	0.84 (0.69–0.87)	0.85 (0.72–0.90)
Marbled cat			0.33 (0.14–0.42)	0.55 (0.25–0.61)	0.44 (0.21–0.48)
Clouded leopard				0.60 (0.48–0.66)	0.81 (0.69–0.85)
Leopard					0.77 (0.69–0.82)

sites were all seven species recorded. Kernel density and trigonometric sum estimates of activity patterns for leopard cat, Asiatic golden cat, clouded leopard, leopard and tiger showed similar patterns within each species (Fig. 2). Large differences between the kernel density and trigonometric sum estimates for fishing cat indicated that sample size was too small to estimate activity reliably (Linkie & Ridout, 2011), and due to sampling constraints we decided to omit this species from comparisons with other species. From the limited data available, marbled cats were completely diurnal ($n = 10$), and fishing cats are at least partly nocturnal ($n = 6$). Leopard cats were strongly nocturnal (85%, $n = 258$). Clouded leopards were mostly nocturnal (73%, $n = 79$). Asiatic golden cats were cathemeral (58% of observations between 0600–1800 hours, $n = 81$), as were tigers (57% of observations between 1800–0600 hours, $n = 198$) which exhibited slight activity peaks at dawn and dusk. Leopards were mostly diurnal (68%, $n = 402$).

We identified 4 pairs of sympatric cats with a high degree of daily activity overlap (estimated overlap coefficients ≥ 0.80); leopard cat and clouded leopard, Asiatic golden cat and leopard, Asiatic golden cat and tiger, clouded leopard and tiger (Table 2). Marbled cat had notably low degrees of overlap (< 0.35) with both leopard cats and clouded leopards (Table 2), although due to the low sample size interpretations should be made with caution.

We had adequate data to explore the variation in activity patterns for Asiatic golden cats and leopard cats, as well as Asiatic golden cats and clouded leopards at Khao Yai National Park (2,168 km²; Fig. 3). In Khao Yai National Park, Asiatic golden cats had a higher overlap with clouded leopards ($\hat{\Delta}_1 = 0.90$; Fig. 3) than with leopard cats ($\hat{\Delta}_1 = 0.63$; Fig. 3). There were limited data to explore the variation in activity pattern overlap for clouded leopards with either leopards or tigers. Tigers had the highest degree of overlap with leopards at Huai Kha Kaeng Wildlife Sanctuary ($\hat{\Delta}_1 = 0.74$; Fig. 4), but the overlap was consistently high across the four study areas, where both species were recorded most often (Fig. 4). All activity records of Tiger at Khao Yai pertain to one individual animal. Since there is so little information on tigers, and Khao Yai is a high profile park and priority for management in the Thai protected area system, we decided

to include the small number of tiger capture records in the analysis. The tiger at Khao Yai National Park (where there are no leopards) was mostly active after dawn (Fig. 4).

DISCUSSION

Our data confirmed that small cats exhibited activity behaviours ranging from strongly nocturnal (leopard cat) through mostly nocturnal (clouded leopard), and mostly diurnal (Asiatic golden cat) to completely diurnal (marbled cat), and suggested that fishing cat behaviour could be completely nocturnal. Although our data comes from a set of reserves in Thailand, our results could be indicative of the general behaviour patterns of cat species in other parts of their range.

From our data and other studies in Thailand (Grassman, 2000; Grassman et al., 2005a; Austin et al., 2007), leopard cats are strongly nocturnal with peaks of activity at dawn and dusk (Figs. 2, 3). Similarly, 77% of leopard cat records from a secondary forest in Peninsular Malaysia (Azlan & Sharma, 2006), and 65% of records at one site in Borneo (Rajaratnam, 2000; Cheyne & McDonald, 2011) were nocturnal. This pattern correlates with the fact the species' major prey, murid rodents, are mostly nocturnal (Roll et al., 2006). Consistent with the study of Austin et al. (2007) at Khao Yai, we found that across sites and at Khao Yai, leopard cat activity overlapped significantly with that of clouded leopards ($\hat{\Delta}_1 = 0.90$; Table 2, Fig. 3).

Our study showed that clouded leopard activity was mainly nocturnal, similar to the studies of Gumal et al. (in press), and Azlan & Sharma (2006) from Peninsular Malaysia, and also Kanchanasaka (2001) from southern Thailand. However, the overall activity pattern from radio telemetry studies ($n = 4$) indicated two peaks at 1800–0200 hours and 0800–1200 hours (Grassman et al., 2005b). It is possible that clouded leopard terrestrial activity is higher at night-time due to the avoidance of leopards but that during daytime they are more active on trees (A. Wilting, pers. comm). Austin et al. (2007) found two radio-collared clouded leopards had peaks of activity at dawn and dusk. Clouded leopard activity showed a very high degree of overlap ($\hat{\Delta}_1 > 0.80$) with that

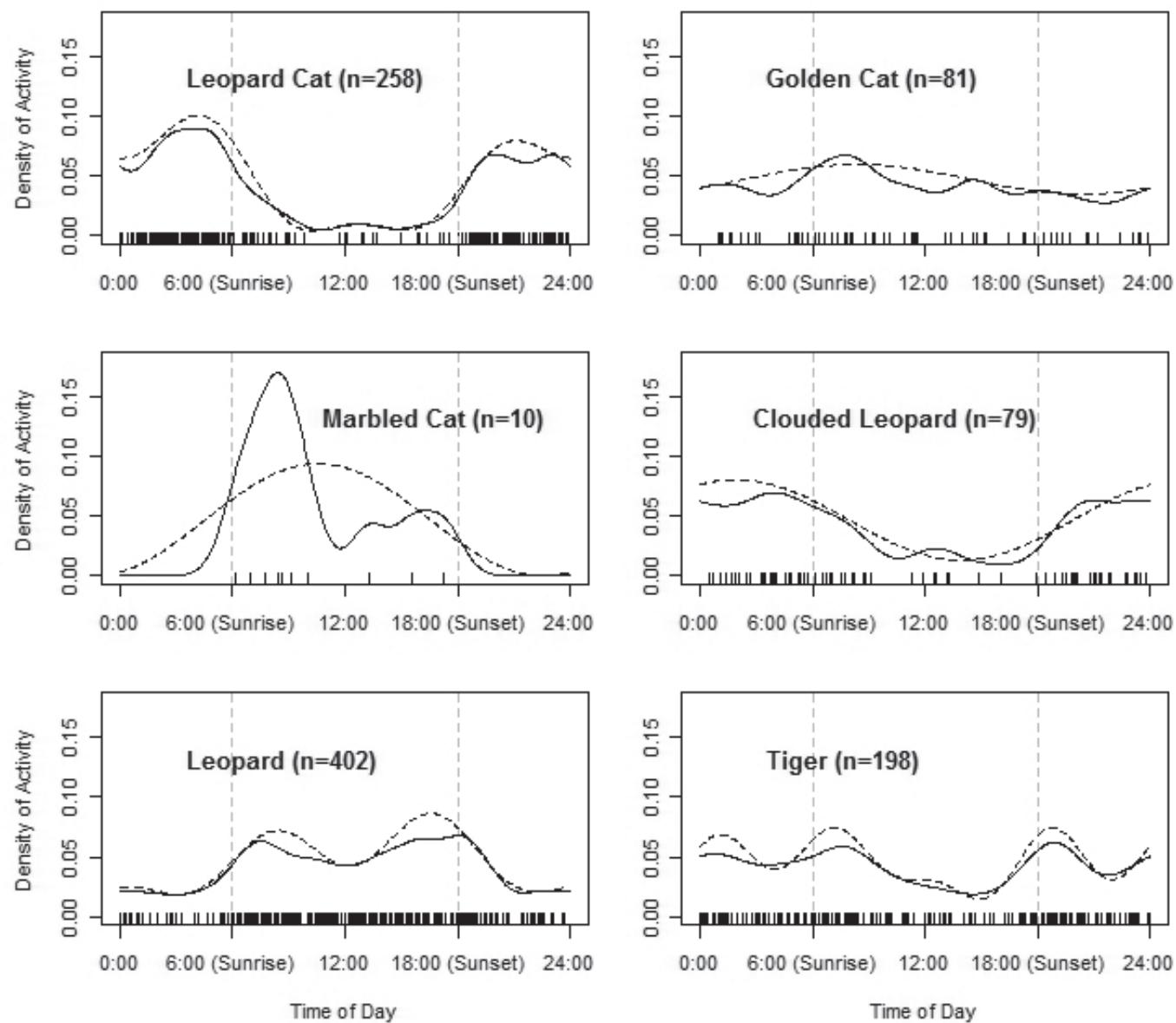


Fig. 2. Density estimates of daily activity patterns of six felid species in Thailand. Solid lines are kernel-density estimates; dashed lines are trigonometric sum distributions. The short vertical lines above the x-axis indicate the times of individual photographs.

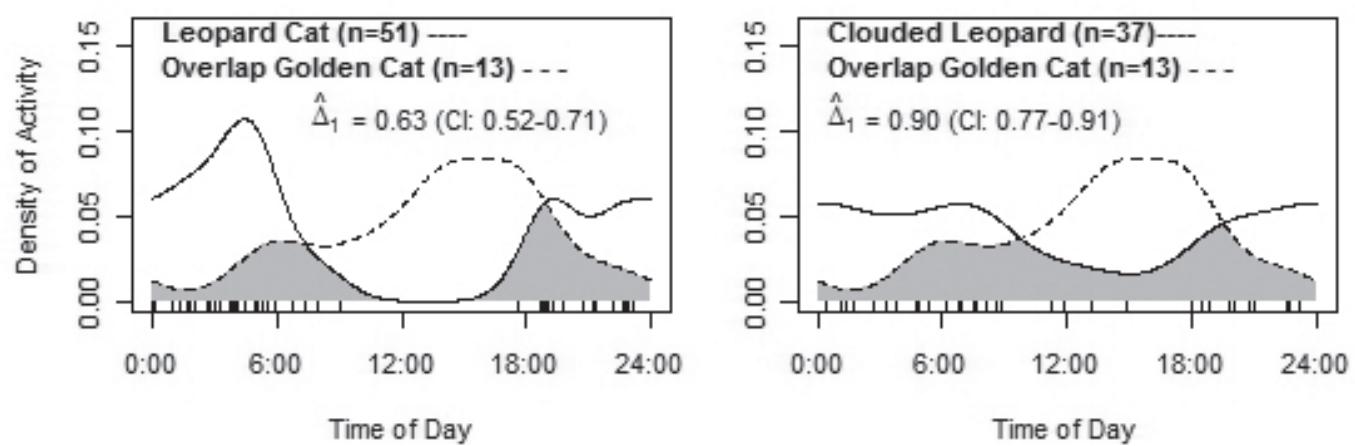


Fig. 3. Daily activity patterns of and overlap of Asiatic golden cat compared to leopard cat and clouded leopard in Khao Yai National Park, Thailand. Individual photograph times are indicated by the short vertical lines above the x-axis. The overlap coefficient is the shaded area under the two density estimates.

of tigers but not that of leopards (Table 2). Activity patterns of its prey, such as muntjacs *Muntiacus* spp., chevrotains *Tragulus* spp. (primarily nocturnal), and wild pigs *Sus* spp. (primarily diurnal; Kawanishi & Sunquist, 2004), which are also preferred prey species of leopards (Ngoprasert et al., 2012), may also influence clouded leopard activity. The activity pattern for Asiatic golden cat across our sites was catemeral with peaks after dawn and during mid-afternoon (1400–1500 hours). At Khao Yai, Asiatic golden cats overlapped with leopard cats at night (Fig. 3). There were multiple peaks of overlap with clouded leopards during the night and daytime (Fig. 3). Fifty-two percent of Asiatic golden cat photo captures were from the period 1900–0500 hours in an unprotected secondary dipterocarp forest where clouded leopards and leopard cats were present (Azlan & Sharma, 2006). Only 31% of Asiatic golden cat records were from the period 1900–0700 hours in a protected primary rainforest (Kawanishi & Sunquist, 2008). Asiatic golden cat activity showed a very high degree of overlap ($\hat{\Delta}_1 > 0.80$; Table 2) with that of both tigers and leopards, but their potential prey species (murid rodents, porcupines, mouse deer, primates, snakes, lizards, and birds; Kawanishi & Sunquist, 2008) are different to the prey species of larger cats, which reduces the possibility of food competition. However, the overlap in activity creates the potential for increased predation risk from the larger cats.

All available marbled cat records ($n = 10$) were from daytime (0600–1800 hours), consistent with the study of Thunhikorn et al. (2008) who obtained four camera-trap photographs of marbled cat during daytime (0630, 0730, 1410, and 1530 hours). Azlan et al. (2009) recorded marbled cats being active at nighttime in Sabah ($n = 2$ sightings), but failed to record them from 1,916 trapnights of camera-trap sampling, while Samejima et al. (2012) working in the same forest reserve recorded 17 detections of marbled cats between Dec. 2007 and Dec. 2010, of which only 3 were detections at night. In Thailand, although sample sizes were small ($n = 10$) marbled cats showed low overlap with leopard cats and clouded leopards ($\hat{\Delta}_1 < 0.35$; Table 2), and moderate overlap with leopards and tigers ($\hat{\Delta}_1 = 0.55$ and 0.44, respectively; Table 2). Marbled cats are believed to be partly or even mainly arboreal with great climbing skills (Azlan et al., 2009), a behaviour which may increase their ecological separation from leopard cats and other ground-dwelling cats (Asiatic golden cat, tiger).

At Khao Sam Roi Yod, cameras were operated only between 1700–0800 hours to prevent theft (Cutter & Cutter, 2009). The small number of records of fishing cat ($n = 6$) from camera-traps there were all between 1900–0500 hours, but additional daytime sampling (and a lack of records during the day) would be required to confirm whether the activity pattern is nocturnal. Records were from habitats that are heavily fragmented, and receive daytime human traffic in various levels of intensity. Therefore, fishing cats may be concentrating their activity at night to avoid human disturbance.

Tigers showed moderately high overlap ($\hat{\Delta}_1 \geq 0.61$) with leopards at Huai Kha Kaeng, Kuiburi, Kaeng Krachan, and in Thung Yai Naresuan; at Khao Yai where leopards are absent, tigers peaked slightly in early morning around 0600 hours (Fig. 4). Since 2001 there have been no new camera-trap records of tigers at Khao Yai and the species is presumed functionally extinct at the site (Jenks et al., 2011). The observations at Huai Kha Khaeng, Kuiburi, Kaeng Krachan, and Thung Yai Naresuan are consistent with other evidence from these sites that in the wild, tiger and leopards consume similar prey species such as wild pig and red muntjac, are active during the same time periods, and therefore potentially compete for food (Ngoprasert et al., 2012).

Evidence from capture-recapture studies suggests that tiger density was highest in Huai Kha Khaeng (>3.5 tigers/100 km²; Simcharoen et al., 2007) followed by Thung Yai Naresuan (1.1–1.5 tigers/100 km²; WCS, 2010), and lowest in Kuiburi (<1 tiger/100 km²; Steinmetz et al., 2009). However, leopard density was highest, at least in Kaeng Krachan (5.4–5.9 leopards/100 km²) and Kuiburi (2.6–4.0 leopards/100 km²)

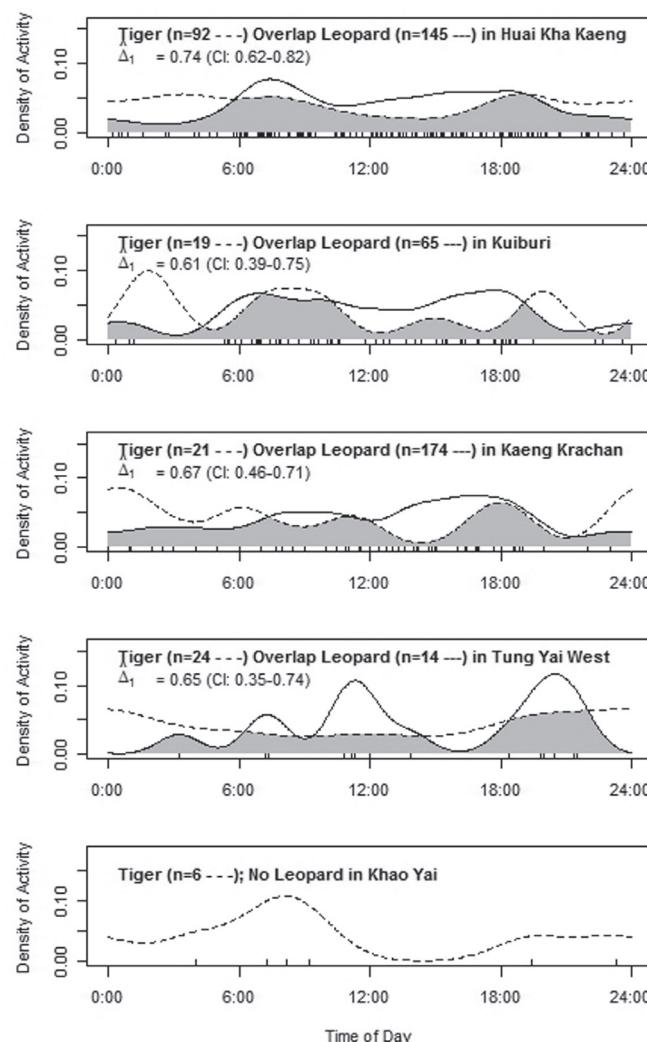


Fig. 4. Daily activity patterns of tigers and leopards in five study areas in Thailand. Individual photograph times are indicated by the short vertical lines above the x-axis. The overlap coefficient is the area under the minimum of the two density estimates, as indicated by the shaded area in each plot.

(D. Ngoprasert, A. J. Lynam, R. Steinmetz, N. Seuaturien & G. Gale, unpublished data) where tiger density is apparently reduced due to poaching (Ngoprasert et al., 2007), and mesopredator release (Moreno et al., 2006) may have occurred. Consequently, we were interested to see whether the two large cats showed different or similar patterns of activity between different sites given varying densities. Tigers and leopards showed complete overlap in activity at Huai Kha Khaeng, with peaks of overlap at dawn and after dusk (Fig. 4.), presumably optimal hunting times for ungulate prey. This suggests the possibility of direct competition for resources as this has been documented in other parts of their distribution where the two co-occur (Schaller, 1967; Seidensticker et al., 1990; Odden et al., 2010; Harihar et al., 2011). Leopards may coexist with tigers by avoiding places where tiger prefer to hunt and rest (Sunquist & Sunquist, 2002) or by partitioning prey by their size (Karanth et al., 1995).

CONCLUSIONS

Activity patterns of small cats elucidated from this study need to be tempered by consideration of the limitations of the data. Most of the surveys targeted tiger and other large mammals, with camera-trap locations and heights optimised to detect them, set mainly along roads and large trails. Smaller cats might use such pathways only as alternate routes of travel, or avoid them during some periods due to their habitual use by larger carnivores (Bitetti et al., 2006), and the possible predation risk (Grassman, 1997). Also, human and vehicular traffic may have profound effects on habitat use by wild cats in protected areas (Rogala et al., 2011; Gubbi et al., 2012). At many of our study sites, trails are used frequently by people, especially those sites receiving heavy tourist traffic (central parts of Khao Yai), or poachers (all sites). Consequently, surveyors targeting small cats using camera-traps should consider placing some of their devices away from main roads and trails onto secondary trails and gaps in understory vegetation (Baker et al., 2011). Some of the species are at least partially, or even predominantly, arboreal. This is especially true for the marbled cat and clouded leopard. Additional insights into the behaviour and interactions of small cats will be revealed through spotlight surveys that include effort in trees (Duckworth et al., 1999), and through radio collar studies (Austin et al., 2007; Grassman et al., 2005b; P. Cutter unpubl. data., 2011), which allow recording of total activity-levels for individual animals. This paper highlights the value of collaboration among researchers and conservation agencies in pulling together datasets to assess ecological characteristics of poorly known tropical wildlife.

ACKNOWLEDGEMENTS

We wish to thank the Clouded Leopard Project, TRF/BIOTEC Special Program for Biodiversity Research and Training Thailand, Kasetsart University, and the Smithsonian Conservation Biology Institute for providing funding for a workshop that brought some of the authors together to

discuss collaboration. S. Kitamura was funded by the Mahidol University Government Research Grant, the National Center for Genetic Engineering and Biotechnology, the Hornbill Research Foundation, and a JSPS Research Fellowship. We thank the Wildlife Conservation Society Thailand, World Wide Fund for Nature—Thailand, and the Smithsonian Conservation Biology Institute for allowing participants to use data collected under their auspices. We also thank R. Phoonjampa, S. Tanasarnpaiboon, and M. Pliwsungnoen for their assistance. Finally we thank two anonymous reviewers for their comments and suggestions which helped improve the final version of the paper.

LITERATURE CITED

Austin, S. C., M. E. Tewes, L. I. Grassman Jr. & N.J. Silvy, 2007. Ecology and conservation of the leopard cat *Prionailurus bengalensis* and clouded leopard *Neofelis nebulosa* in KhaoYai National Park, Thailand. *Acta Zoologica Sinica*, **53**:1–14.

Baker, M. C., W. J. McShea, A. J. Lynam, N. Bhumpakpan & J. Howard, 2011. Taphraya National Park, Thailand—A unique and neglected protected area and the species that call it home. *Abstracts of the 91st Annual Meeting of the American Society of Mammalogists: A Joint Meeting with the Australian Mammalian Society*. Portland, USA.

Bitetti, M. S. D., A. Paviolo & C. D. Angelo, 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. *Journal of Zoology*, **270**: 153–163.

Cheyne, S. M. & D. W. McDonald, 2011. Wild felid diversity and activity patterns in Sabangau peat-swamp forest, Indonesian Borneo. *Oryx*, **45**: 119–124.

Cutter, P. & P. Cutter, 2009. Recent sightings of fishing cats in Thailand. *Cat News*, **51**: 26–27.

DNP, 2010. *Statistical Data on Forest Landuse*. <http://www.dnp.go.th/statistics/2553/stat2553.asp>. (Accessed 19 May 2012). (Text in Thai).

Duckworth, J. W., R. E. Salter & K. Khounboline (eds.), 1999. *Wildlife in Lao PDR: 1999 Status Report*. IUCN–The World Conservation Union, Wildlife Conservation Society, and Centre for Protected Areas and Watershed Management, Vientiene, Lao PDR. 275 pp.

FAO, 2010. *Global Forest Resources Assessment. Main Report. No. 163*. Rome, Italy. 377 pp. <http://www.fao.org/forestryfra/fra2010/en/>. (Accessed 19 May 2012).

Fernandez-Duran, J. J., 2004. Circular distributions based on nonnegative trigonometric sums. *Biometrics*, **60**: 499–503.

Grassman, L. I., Jr., 1997. *Ecology and Behavior of Four Sympatric Carnivore Species (Mammalia :Carnivora) in Kaeng Krachan National Park, Thailand*. Unpublished MSc thesis, Kasetsart University, Bangkok. 94 pp.

Grassman, L. I., Jr., 2000. Movements and diet of the leopard cat *Prionailurus bengalensis* in a seasonal evergreen forest in south-central Thailand. *Acta Theriologica*, **45**: 421–426.

Grassman, L. I., Jr., M. E. Tewes, N. J. Silvy & K. Kreetiyutanont, 2005a. Spatial organization and diet of the leopard cat (*Prionailurus bengalensis*) in north-central Thailand. *Journal of Zoology London*, **266**: 45–54.

Grassman, L. I., Jr., M. E. Tewes, N. J. Silvy & K. Kreetiyutanont, 2005b. Ecology of three sympatric felids in a mixed evergreen forest in north-central Thailand. *Journal of Mammalogy*, **86**: 29–38.

Gray, T. N. E. & C. Phan, 2011. Habitat preferences and activity patterns of the larger mammal community in Phnom Prich Wildlife Sanctuary, Cambodia. *Raffles Bulletin of Zoology*, **59**: 311–318.

Gubbi, S., H. C. Poornesha & M. D. Madhusudan, 2012. Impact of vehicular traffic on the use of highway edges by large mammals in a South Indian wildlife reserve. *Current Science*, **102**: 1047–1051.

Gumal, M., A. B. B. M. Salleh, M. N. Yasak, L. S. Horng, B. P. Y-H. Lee, L. C. Pheng, H. Hamzah, D. Kong, D. Magintan, D. T. C. Yung, A. Z. B. Zalaluddin, A. B. Azmi, N. B. Khalid, T. P. Yen, V. Mufeng, F. C. F. Meng & S. Ng, (in press). Non-Panthera cats in the Endau Rompin landscape in Johor. *Cat News*.

Harihar, A., B. Pandav & S. P. Goyal, 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. *Journal of Applied Ecology*, **48**: 806–814.

Jenks, K., P. Chanteap, K. Damrongchainarong, P. Cutter, P. Cutter, T. Redford, A. J. Lynam, J. Howard & P. Leimgruber, 2011. A case study for basic camera-trap monitoring in tropical protected areas. *Tropical Conservation Science*, **4**: 113–131.

Kanchanasaka, B., 2001. Diversity and distribution of carnivores in Khlong Saeng Wildlife Sanctuary. In: Wildlife Research Division's Annual Report. National Parks ,Wildlife and Plant Conservation Department, Bangkok, Thailand. Pp. 118–137. (Text in Thai).

Karanth, K. U. & M. E. Sunquist, 1995. Prey selection by tiger, leopard, and dhole in tropical forests. *Journal of Animal Ecology*, **64**: 439–450.

Kawanishi, K. & M. E. Sunquist, 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. *Biological Conservation*, **120**: 329–344.

Kawanishi, K. & M. E. Sunquist, 2008. Food habits and activity patterns of the Asiatic golden cat (*Catopuma temminckii*) and dhole (*Cuon alpinus*) in primary rainforest of Peninsular Malaysia. *Mammal Study*, **33**: 173–177.

Kitamura, S., S. Thong-Aree, S. Madsri & P. Poonswad, 2010. Mammal diversity and conservation in a small isolated forest in Thailand. *Raffles Bulletin of Zoology*, **58**: 145–156.

Laidlaw, R. & W. N. W. Shaharuddin, 1998. Activity patterns of the Indochinese tiger (*Panthera tigris corbetti*) and prey species in Peninsular Malaysia. *Journal of Wildlife & Parks (Malaysia)*, **16**: 85–96.

Linkie, M. & M. S. Ridout, 2011. Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology*, **284**: 224–229.

Mohd-Azlan, J. M. & D. S. K. Sharma, 2006. The diversity and activity patterns of wild cats in a secondary forest in Peninsular Malaysia. *Oryx*, **40**: 36–41.

Mohd-Azlan, J. M., H. Samejima & A. Wilting, 2009. Records of five Bornean cat species from Deramakot Forest Reserve in Sabah, Malaysia. *Cat News*, **51**: 12–15.

Moreno, R. S., R. W. Kays & R. Samudio, 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *Journal of Mammalogy*, **87**: 808–816.

Ngoprasert, D., A. J. Lynam & G. A. Gale, 2007. Human disturbance affects habitat use and behaviour of a tropical large carnivore in Kaeng Krachan National Park, Thailand. *Oryx*, **41**: 343–351.

Ngoprasert, D., A. J. Lynam, R. Sukmasuang, N. Tantipisanuh, W. Chutipong, R. Steinmetz, K. E. Jenks, G. A. Gale, L. I. Grassman, S. Kitamura, J. Howard, P. Cutter, P. Cutter, P. Leimgruber, N. Songsasen & D. H. Reed, 2012. Occurrence of three felids across a network of protected areas in Thailand: Prey, intraguild, and habitat associations. *Biotropica*, **10.1111/j.1744-7429.2012.00878.x**.

Odden, M., P. Wegge & T. Fredriksen, 2010. Do tigers displace leopards? If so, why? *Ecological Research*, **25**: 875–881.

R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.

Rabinowitz, A., 1989. The density and behavior of large cats in a dry tropical forest mosaic in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Natural History Bulletin of the Siam Society*, **37**: 235–251.

Rabinowitz, A., 1991. Behaviour and movements of sympatric civet species in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Journal of Zoology*, **223**: 281–298.

Rajaratnam, R., 2000. Ecology of the leopard cat (*Prionailurus bengalensis*) in Tabin Wildlife Reserve, Sabah, Malaysia. Unpublished PhD thesis, Universiti Kebangsaan Malaysia, Bangi, Malaysia.

Rajaratnam, R., M. Sunquist, L. Rajaratnam & A. Laurentius, 2007. Diet and habitat selection of the leopard cat (*Prionailurus bengalensis borneoensis*) in an agricultural landscape in Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, **23**: 209–217.

Ray, J. C. & M. E. Sunquist, 2001. Trophic relations in a community of African rainforest carnivores. *Oecologia*, **127**: 395–408.

Ridout, M. S. & M. Linkie, 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, **14**: 322–327.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill & M. Musiani, 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecology and Society*, **16**: 16. <http://dx.doi.org/10.5751/ES-04251-160316>.

Roll, U., T. Dayan & N. Kronfeld-Schor, 2006. On the role of phylogeny in determining activity patterns of rodents. *Evolutionary Ecology*, **20**: 479–490.

Samejima, H., R. Ong, P. Lagan & K. Kitayama, 2012. Camera-trapping rates of mammals and birds in a Bornean tropical rainforest under sustainable forest management. *Forest Ecology and Management*, **270**: 248–256.

Schaller, G. B., 1967. *The Deer and the Tiger*. University of Chicago Press, Chicago, USA. 384 pp.

Scognamillo, D., I. E. Maxit, M. Sunquist & J. Polisar, 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *Journal of Zoology, London*, **259**: 269–279.

Seidensticker, J., M. E. Sunquist & C. McDougal, 1990. Leopards living at the edge of Royal Chitwan National Park, Nepal. In: Daniel, J. C. & J. S. Serrao (eds.), *Conservation in Developing Countries: Problems and Prospects*. Bombay Natural History Society, Bombay. Pp. 415–423.

Simcharoen, S., A. Pattanavibool, K. U. Karanth, J. D. Nichols & N. S. Kumar, 2007. How many tigers *Panthera tigris* are there in Huai Kha Khaeng Wildlife Sanctuary, Thailand? An estimate using photographic capture–recapture sampling. *Oryx*, **41**: 447–453.

Steinmetz, R., N. Seuaturien, W. Chutipong & B. Poonnill, 2009. *The Ecology and Conservation of Tigers and their Prey in Kuiburi National Park, Thailand*. WWF Thailand, and Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand. 58 pp.

Steinmetz, R., D. L. Garshelis, W. Chutipong, & N. Seuaturien, in press. Foraging ecology and coexistence of Asiatic black bear bears and sun bears in a seasonal tropical forest in Southeast Asia. *Journal of Mammalogy*.

Sunquist, F. & M. Sunquist, 2002. *Tiger Moon; Tracking the Great Cats of Nepal*. University of Chicago, Chicago, USA. 187 pp.

Tantipisanuh, N., W. Chutipong, D. Ngoprasert, A. J. Lynam, R. Steinmetz, R. Sukmasuang, K. E. Jenks, L. I. Grassman Jr., P. Cutter, S. Kitamura, N. Bhumpakphan, G. A. Gale & D. H. Reed, in press. Recent distribution records of small cats in Thailand with notes on possible threats and conservation priorities. *Cat News*.

Terborgh, J., 1992. Maintenance of diversity in tropical forests. *Biotropica*, **24**: 283–292.

Thunhikorn S., S. Sothornchit, P. Buakaew, A. Kayankij & S. Lakaew, 2008. *Wildlife Research Division's Annual Report*. National Parks, Wildlife and Plant Conservation Department, Bangkok, Thailand. Pp. 41–50. (Text in Thai).

van Schaik, C. P. & M. Griffiths, 1996. Activity periods of Indonesian rain forest mammals. *Biotropica*, **28**: 105–112.

WCS, 2010. *Recovering Wild Tigers in Thailand's Western Forest Complex: 5-Year (2006–2010) Executive Progress Report*. Bangkok, Thailand. 24 pp.