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# Individual-level movement and space use of Sunda clouded leopards revealed by GPS telemetry and camera traps in a human-modified Bornean landscape

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## Abstract

High-resolution telemetry can reveal how elusive carnivores move and use space in fragmented, human-modified landscapes. The Sunda clouded leopard (*Neofelis diardi*), a forest-dependent felid endemic to Borneo and Sumatra, remains among the least-studied large tropical carnivores, with very limited individual-level movement data. We present the first high-resolution GPS telemetry dataset for the species, using 20-min GPS fixes from four collared adults, integrated with concurrent long-term camera-trap surveys to examine individual space use, movement, diel activity, and patterns of site sharing in a multiple-use landscape in Malaysian Borneo. Home-range estimates, based on three individuals monitored for 39–103 days and derived using multiple estimators, showed that two adult males occupied similar (~41 km² each; 100% k-LoCoH) and largely exclusive (~8% intra-male overlap) ranges that were constrained to forest, whereas kernel density estimation (KDE) and 95% minimum convex polygons (MCP) estimates were several-fold larger and extended beyond forest boundaries. A tracked female occupied a smaller range (~7 km²; k-LoCoH) that overlapped extensively with one male (68.5%) and to a lesser extent with another (20.9%). Camera trap surveys yielded 264 independent detections of nine individuals (four males, five females), with detections across camera stations predominantly solitary (>85% of 30–60-day station-windows). However, a single forested ridgeline in an otherwise largely flat floodplain emerged as a marked hotspot (>50% of detections), repeatedly visited by multiple individuals and containing most observed scent-marking events, indicating that this ridgeline functions as a communication site. Telemetry revealed cathemeral movement characterised by short travel bouts interspersed with prolonged stationary periods concentrated in forest; males moved up to 13 km day$^{-1}$ and travelled faster through oil palm and along roads (0.68–1.49

km $h^{-1}$) than in forest (0.37–0.53 km $h^{-1}$). Camera-trap data indicated dawn activity peaks in both sexes and a dusk peak in females ($\Delta_4$ = 0.74). These results provide a descriptive, individual-level account of movement and space use, and demonstrate how integrating GPS telemetry with camera-trap detections can inform movement ecology for rare carnivores in complex, human-modified landscapes.

## Keywords

Sunda clouded leopard, home range, Spatial ecology, GPS telemetry, camera trapping, kernel density estimation, LoCoH

## Background

Understanding how solitary carnivores use space and time is a core concern of movement ecology and informs interpretation of individual behaviour in heterogeneous landscapes (Macdonald et al., 2010). Spatial partitioning—whether through territorial exclusion, temporal avoidance, or asynchronous use of shared sites—allows individuals to reduce direct conflict, access resources efficiently, and balance competing demands such as foraging, reproduction, and risk avoidance (Maher & Lott, 1995). Among large carnivores, patterns of space use are often influenced by sex, reproductive status, prey availability, and landscape structure (Sandell, 1989; Gittleman & Harvey, 1982). While these dynamics are well documented for temperate systems and well-studied species, they remain poorly understood for rare or cryptic carnivores in tropical ecosystems, where logistical constraints have historically limited access to high-resolution movement data.

Felids, though typically described as solitary, exhibit a wide range of space-use strategies that reflect ecological context and sex-based roles (Sunquist & Sunquist, 2002). In many species, males occupy larger ranges that overlap those of multiple

females, while females often maintain smaller, more exclusive ranges, particularly during reproduction (Sandell, 1989). Even where spatial exclusivity appears strong, individuals may engage in asynchronous spatial overlap, using shared areas at different times to avoid direct encounters while still accessing key resources (e.g. Harmsen et al., 2009). Indirect social interactions are frequently mediated by repeated use and scent marking of shared communication sites (Allen et al., 2016), and such spatiotemporal strategies may be especially important in linear or human-modified landscapes such as riparian corridors or forest–agriculture mosaics (Tucker et al., 2018; Hearn et al., 2018a).

Despite its ecological importance in Borneo, the Sunda clouded leopard (*Neofelis diardi*) remains comparatively understudied, particularly with respect to fine-scale spatial behaviour. Its elusive nature, partly arboreal habits, and naturally low densities have long limited direct observation and individual-level monitoring. As a result, most ecological information on the species has been derived from camera-trap surveys focusing on habitat associations, activity patterns, and population metrics (e.g. Wilting et al., 2012; Hearn et al., 2013; Macdonald & Bothwell, 2018). While studies of diel activity and temporal overlap with prey and sympatric felids have yielded valuable insight into broad-scale behavioural patterns (e.g. Ross et al., 2013; Hearn et al., 2018b), such approaches lack the spatial resolution required to examine individual movement paths and space use over time.

To date, only two published studies have reported movement data from collared Sunda clouded leopards: Hearn et al. (2013), based on VHF telemetry from a single individual, and Hearn et al. (2018a), which incorporated GPS telemetry to model habitat use and landscape connectivity. Neither study examined fine-scale movement

paths, temporal dynamics of space use, or patterns of spatial overlap among individuals.

In this study, we use high-resolution GPS telemetry in combination with long-term camera-trap data to describe space use, movement, diel activity, and site sharing in Sunda clouded leopards inhabiting the Kinabatangan floodplain in eastern Sabah, Malaysian Borneo. This landscape has been extensively modified by oil palm expansion and infrastructure development, resulting in a largely linear network of protected forests, riparian reserves, and degraded corridors that impose strong spatial constraints on animal movement (Abram et al., 2014). We characterise individual home-range use, habitat-specific movement, spatial and temporal overlap between tracked individuals, and patterns of shared site use detected by camera traps. Given the logistical challenges of capturing and collaring this species, telemetry datasets are necessarily limited in sample size and duration; accordingly, this study is explicitly descriptive, aiming to characterise individual-level movement and space use rather than to test hypotheses or infer population-level processes. By clearly delineating this scope of inference, we provide a transparent baseline for future comparative and hypothesis-driven telemetry studies in more continuous forest systems.



## Methods

### *Study Area*

Our study focused on a ~2,000 km² region of the Lower Kinabatangan floodplain in eastern Sabah, Malaysian Borneo, encompassing much of the Lower Kinabatangan Wildlife Sanctuary (LKWS), the Gomantong and Pin Supu Forest Reserves, and the surrounding oil palm-dominated landscape (Figure 1). The LKWS comprises a network

of protected riparian forest blocks embedded within a broader human-modified landscape, while the Gomantong and Pin Supu Forest Reserves are commercially managed forest reserves. Approximately 520 $km^2$ (26%) of this area comprises forest, with the remainder largely consisting of oil palm plantations and associated human-modified habitats. This region's climate is tropical, with average monthly temperatures ranging from 21–34°C and annual rainfall of about 3,000 mm (Ancrenaz et al., 2004).

The floodplain is home to diverse forest ecosystems, including mangroves, flooded forests, and dry (humid) forests (Abram et al., 2014). Poorly drained areas are characterised by low-stature forests, grasslands, and reed swamps, whereas better-drained zones along riverbanks and elevated limestone ridges support riparian and mixed dipterocarp forest. In contrast to the predominantly flat, low-elevation terrain of the LKWS floodplain, the Gomantong and Pin Supu Forest Reserves are largely composed of elevated, topographically rugged limestone forest formations. Within the LKWS itself, isolated limestone ridges occur only rarely along the river margin. One such feature, Batangan ridge in Lot 5, is a short (~200 m long) limestone ridgeline rising approximately 50 m above the surrounding floodplain forest, forming the only prominent area of raised terrain along the river section between Pin Supu and Lot 5. Oil palm (*Elaeis guineensis*) plantations dominate much of the floodplain, ranging from newly cleared lands and young plantings with sparse canopy cover to mature plantations (7–24 years old) with relatively dense canopy layers (Abram et al., 2014). Forest areas that have escaped conversion have been repeatedly logged over the past century but remain important habitat for numerous threatened species, including the Sunda clouded leopard. Much of the privately owned forest remains earmarked for future oil palm expansion (Abram et al., 2014).

A network of gravel roads and tracks is present throughout oil palm plantations to facilitate agricultural management. In contrast, sealed roads are limited to two main routes: the A5 highway, which runs approximately north–south and bisects the Pin Supu Forest Reserve, and an east–west road north of the LKWS that terminates at Kampung Sukau (Figure 1). The A5 experiences relatively heavy traffic during daylight hours but is infrequently used at night, whereas the Sukau road remains quieter at all times.

### *Sunda clouded leopard live capture and GPS collar deployment*

Between 3 May 2013 and 28 September 2014, we deployed custom-built, doubled-ended, steel mesh box traps (1×1×3 m) at six locations within Lots 5 and 6 of the LKWS and the adjacent Pin Supu Forest Reserve (Figure 1), with distances between traps ranging from 200 m to 18 km, to capture Sunda clouded leopards for GPS collaring. Traps were unbaited and positioned along identified clouded leopard travel routes and continuously monitored using one or two passive infrared camera traps (Reconyx HC800, Reconyx Inc., WI, USA) and through in-person inspections conducted daily or twice daily. All trapping and animal handling procedures followed protocols developed jointly by our research team and the Sabah Wildlife Department. A licensed veterinarian was present throughout all capture and handling activities to supervise procedures and ensure animal welfare. None of the captured individuals showed external injuries due to capture or handling (Nájera and Hearn, 2022). Detailed methodologies for trapping and immobilization are provided in Hearn et al. (2018a), Nájera et al. (2017), and Nájera and Hearn (2022).

We fitted captured individuals with GPS-GSM collars (Lotek WildCell SD/SL, Lotek Wireless Inc., Ontario, Canada), equipped with automated drop-off devices

programmed to release after the expected battery life of 32 weeks. We programmed collars to record GPS fixes at 20-minute intervals, balancing the aim of capturing fine-scale movement patterns with maximising battery life to extend deployment duration, given the rarity of high-resolution telemetry data for this species. Prior to field deployment, we assessed the accuracy of two collars over a 24-hour period by comparing recorded fixes to true locations determined with a handheld GPS unit (GPSmap 62, Garmin Ltd., Kansas, USA). The mean ± SE Euclidean distance error was 9.5 ± 0.9 m (range: 1.3–23.7 m; n = 152). Following established standards (e.g. Frair et al., 2010), for all subsequent analyses, we excluded location fixes with a dilution of precision (DOP) >8 and removed visually apparent outliers.

*Camera trap survey*

Between 2010 and 2014, we conducted intermittent, phased camera-trap surveys in the central Kinabatangan floodplain (Figure 1). The first intensive phase occurred from 24 July to 17 December 2010, during which 70 camera stations were deployed throughout the LKWS and the Pin Supu and Gomantong Forest Reserves, covering approximately 89 km². A second intensive phase was conducted from 29 April 2013 to 18 November 2014, largely replicating Phase 1 deployments and expanding the network to a total of 90 camera stations covering approximately 101 km². During the intervening period, cameras were intermittently deployed at 22 camera stations along an approximately 21 km section of the north bank of the Kinabatangan River within Lot 5 of the LKWS, encompassing approximately 39 km².

We used passive infrared camera traps (Reconyx HC500 and PC800 models; Reconyx Inc., Holmen, Wisconsin, USA) deployed along riparian trails formed by human and elephant activity and along ridgelines where terrain permitted. Cameras were

deployed in pairs at an average spacing of 1.21 km (range 0.63–2.34 km) and mounted approximately 30 cm above ground. Cameras operated continuously (24 h $day^{-1}$) and were programmed to capture bursts of three images per trigger event at high sensitivity with no delay between triggers. Infrared flash was used at night to minimise disturbance. Cameras were periodically checked to ensure functionality, and images were downloaded for processing. We identified and sexed individual Sunda clouded leopards based on pelage patterns and morphology. We retained only independent capture events for analysis, defined as one record per individual per camera station within a 30-minute interval.

Camera placement targeted wildlife travel routes and ridgelines rather than randomly distributed locations, and stations therefore do not represent unbiased samples of habitat availability. Camera-trap data are interpreted here as indices of site use and spatiotemporal overlap rather than as measures of detection probability, activity rate, or abundance.



### *Home range*

Using telemetry data, we estimated clouded leopard home ranges using the package adehabitatHR version 0.4.16 (Calenge, 2006) in R (R Core Team, 2024), applying three commonly used methods: the Local Convex Hull (LoCoH), kernel density estimation (KDE), and minimum convex polygons (MCP). LoCoH constructs convex hulls around local clusters of points to delineate range boundaries, KDE estimates a smoothed utilisation distribution across space, and MCP defines the outermost extent of recorded locations. These approaches differ in how they represent space use, particularly in heterogeneous or fragmented landscapes, where KDE may overestimate space use (Getz et al., 2007).

We computed LoCoHs (100% utilisation distribution) using the k-method, selecting the smallest k value that filled spurious holes in the core area, following Lyons et al. (2013). For KDE, we calculated 95% and 50% kernel utilisation distributions (KUDs) using the reference bandwidth (href) to estimate total and core home range sizes and we calculated 95% and 50% MCPs to facilitate comparison with previous studies.

As a boundary-based method, k-LoCoH provides a conservative representation of space use by limiting inclusion of areas not supported by observed locations, whereas KDE and MCP can incorporate unused space due to smoothing and boundary effects. Accordingly, we used 100% LoCoH ranges to represent the full extent of observed space use and report 95% and 50% KDE and MCP isopleths to facilitate comparison with commonly reported total and core home ranges and to reduce sensitivity to peripheral locations.

We calculated pairwise home range overlaps between individuals as the proportion of one individual's k-LoCoH home range intersecting that of another. Home range estimates reflect utilisation during the collar deployment period and are interpreted as sampling-period ranges rather than as annual home ranges.

To facilitate comparison with previous camera-trap studies, we also derived exploratory estimates of spatial extent from camera-trap detections. For individuals recorded at ≥3 camera stations within each survey period (Phase 1, intervening period, and Phase 2), we calculated 100% MCPs based on the spatial locations of camera stations at which each individual was detected. Trimmed MCPs (e.g. 95%) were not calculated due to the small number of unique detection sites per individual, which would result in unstable and inconsistent estimates. These camera-based MCPs are presented as coarse indices of spatial extent and interpreted cautiously.

*Path-level movement and stationary periods*

To quantify movement patterns, we calculated straight-line distances between consecutive GPS collar locations, typically separated by 20 minutes. We classified activity as either moving (distance >9.5 m, exceeding the mean location error and indicating directional progression) or stationary (distance <9.5 m, with no consistent directional progression). We grouped consecutive movement or stationary observations into travel bouts and stationary periods, respectively. Because fix intervals occasionally varied due to dropped locations, this threshold provides a conservative operational definition of movement and may underestimate fine-scale activity during periods of reduced fix acquisition. Stationary periods may therefore represent resting behaviour or limited movement such as stalking, prey observation, or feeding.

For each travel bout, we calculated duration, cumulative distance moved (sum of 20-minute interval distances), and movement speed. Daily distance moved was calculated using two approaches: (1) summing all travel bout distances within a 24-hour period, and (2) calculating the Euclidean distance between the first recorded locations on consecutive days to facilitate comparison with previous felid movement studies. Mean stationary period duration was also calculated.

We assigned each travel bout and stationary period a habitat classification using a land-use GIS dataset developed by Abram et al. (2014). The original 16 habitat types were reclassified into three primary categories: forest, open-canopy oil palm, and closed-canopy oil palm. Open-canopy oil palm comprised under-productive plantations with sparse tree cover, often associated with prolonged flooding, whereas closed-canopy oil palm consisted of mature plantations with dense canopy cover

(Abram et al., 2014). A fourth category, roads, was assigned to travel bouts intersecting sealed roads identified using high-resolution satellite imagery (Google Earth, 2024). Travel bouts traversing multiple habitat types were subdivided accordingly, and the number of stationary periods recorded in each habitat type was quantified.

### *Co-occurrence at camera stations*

Using camera-trap data, we assessed spatiotemporal overlap among Sunda clouded leopards at shared sites. We applied a fixed-window approach using non-overlapping 30 and 60-day intervals to capture shorter- and longer-term patterns of site use. We selected these window lengths pragmatically while acknowledging their arbitrary nature. We applied time windows sequentially from the first detection date across the sampling period.

Within each window and for each camera station, we defined group composition as the number and sex of unique individuals detected (e.g. “1 male”, “2 males”, “1 male, 1 female”). Each station-window combination contributed a single group composition category based on all detections during that interval. Co-occurrence within a window does not imply simultaneous presence or direct interaction, but rather repeated use of the same site by multiple individuals over the specified period. Frequencies of group compositions were expressed as percentages of all detection windows. We also recorded instances of scent-marking behaviour from camera-trap images and summarised their frequency across stations. Because the camera station located on the Batangan ridge yielded disproportionately high Sunda clouded leopard detection frequencies, we analysed this focal ridgeline separately to examine whether patterns

of site sharing and scent-marking behaviour differed from those observed across the remaining stations (n = 109).

### *Temporal activity*

Camera-trap detections were used to examine diel activity patterns of male and female Sunda clouded leopards and to quantify temporal overlap between sexes. Analyses followed Ridout and Linkie (2009) using the R package Overlap (Linkie & Ridout, 2011; Meredith & Ridout, 2016). We estimated activity patterns using non-parametric kernel density estimation with a circular (von Mises) distribution and a default bandwidth of 1.0. We summarised activity density for dawn (05:00–07:00), day (07:00–17:00), dusk (17:00–19:00), and night (19:00–05:00). We quantified temporal overlap between sexes using the coefficient of overlap, $\Delta_4$ (Ridout & Linkie, 2009), with 95% confidence intervals derived from 10,000 smoothed bootstrap samples.



## Results

### *Sunda clouded leopard capture and collaring data*

Live trapping resulted in the capture of three adult male and two adult female Sunda clouded leopards. These individuals represented all males and two of the four females detected in the study area during concurrent camera-trap surveys. One female (CLF3) was captured twice but was assessed to be elderly and in suboptimal physical condition and was therefore released without collaring. Collar deployment durations varied among individuals due to premature device failures, with functional periods ranging from 6 to 103 days (Table 1).

### *Camera trap survey*

A total of 264 independent photographic records of Sunda clouded leopards was obtained, comprising 138 male and 122 female detections. These records represented nine individuals (five females and four males). All four collared individuals were photographed during camera-trap deployments, and five additional individuals were detected only via camera traps. Four records could not be confidently assigned to individuals due to poor image quality. Sampling effort and detection rates varied substantially among survey periods (Figure 5). During Phase 1 (2010), 4,340 trap nights yielded 31 records, including three females (n = 22; one accompanied by a juvenile) and two males (n = 9). During the lowered intensity intervening period, 2054 trap nights yielded 114 records, including five females (n = 54; one accompanied by a juvenile), three males (n = 56) and four unidentifiable records. Phase 2, which involved expanded and more consistent sampling effort, produced 119 records from 6046 trap nights, including four females (n = 44), three males (n = 71) and four unidentifiable records.

*Home range*

Home-range estimates for individuals monitored for 39–103 days varied substantially among analytical methods (Table 1; Figure 2). For all individuals with sufficient data, KDE and MCP estimates were markedly larger than those derived using k-LoCoH, and frequently extended into non-forested areas. The two adult males (CLM3 and CLM4) exhibited similar home-range sizes despite differing collar durations, although absolute values differed considerably. Using k-LoCoH, both males occupied areas of approximately 41 km², whereas 95% KDE estimates ranged from 162.8 to 175.1 km² and 95% MCP estimates from 118.7 to 199.7 km². The collared female (CLF4) occupied a smaller area than males across all estimators, with a k-LoCoH range of 7.0

km² and corresponding 95% KDE and MCP estimates of 67.8 km², respectively. Due to the short sampling duration, home-range size was not estimated for CLM1.

CLM3 and CLM4 occupied largely distinct home ranges with minimal spatial overlap. CLM3's range was predominantly linear, extending westward along the Kinabatangan River from the Batangan ridge in Lot 5 to the Pin Supu Forest Reserve. In contrast, CLM4's range lay to the north and east, encompassing the eastern riparian boundary of Lot 5 and much of the Gomantong Forest Reserve. Spatial overlap between the two males was limited to approximately 8% of each individual's k-LoCoH home range and was concentrated around the Batangan ridge (Figure 2b,d; Table 2). The collared female (CLF4) overlapped extensively with CLM4 (68.5% of her range), sharing space in both the Batangan ridge and the Gomantong Forest Reserve, and to a lesser extent with CLM3 (20.9%), with shared areas confined to Batangan. Movement data from CLM1 indicated that he also visited Batangan ridge and used a riparian corridor west of the ridge similar to that used by CLM4.

For comparison, exploratory MCPs derived from camera-trap detections (100% MCP) varied widely among individuals and survey periods, and often differed from telemetry-derived MCP estimates. For some individuals, camera-based MCPs were of a similar order of magnitude to telemetry estimates, whereas for others they were substantially smaller or larger, reflecting differences in the number and spatial distribution of camera stations (Table S1).

### *Path-level movement and stationary periods*

Across all recorded travel bouts, mean daily distance travelled by the three collared males ranged from 3.18 to 4.12 km, with daily values ranging from below the GPS error threshold (i.e. no discernible movement) to a maximum of 13.03 km (Table 3).

The collared female moved less than males, with a mean daily distance of 2.08 km and a maximum recorded daily distance of 6.14 km. For all individuals, minimum straight-line distances between consecutive-day locations were consistently lower than estimates derived from summing all travel bouts (Table 3).

Mean travel-bout durations were 2.1 h (n = 261, SD = 2.0, range = 0.3–11.0 h) for CLM3 and 1.3 h (n = 253, SD = 1.8, range = 0.3–12.7 h) for CLM4. Most travel bouts were short, with strongly right-skewed duration distributions, and this pattern was consistent during both diurnal and nocturnal periods (Figure 3).

A total of 516 stationary periods were identified, comprising 261 for CLM3 and 255 for CLM4. Mean stationary-period duration was 6.1 h (SD = 10.3, range = 0.3–93.7 h) for CLM3 and 2.3 h (SD = 3.3, range = 0.3–32.0 h) for CLM4. Stationary periods were overwhelmingly associated with forest habitat. CLM3 spent 98.9% (n = 258) of stationary periods in forest and 1.1% (n = 3) in closed-canopy oil palm, with none recorded in open-canopy oil palm. All stationary periods for CLM4 occurred within forest habitat.



Movement bouts were most frequently recorded in forest for both males (CLM3: n = 276; CLM4: n = 257), with fewer bouts occurring in oil palm and on roads. CLM3 recorded 22 bouts in oil palm and five on roads, while CLM4 recorded six oil-palm bouts and three road crossings. Only one travel bout for CLM1 occurred in oil palm, and all recorded travel bouts for the collared female (CLF4) occurred within forest habitat. Across all habitats, males generally moved faster than the female (Table 4). For CLM3 and CLM4, movement speeds were higher in oil palm and on roads than in forest. CLM3 moved at mean speeds of 0.91 km $h^{-1}$ in oil palm and 1.49 km $h^{-1}$ on roads, compared with 0.53 km $h^{-1}$ in forest, while CLM4 moved at 1.05 km $h^{-1}$ in oil

palm and 0.68 km $h^{-1}$ on roads, compared with 0.37 km $h^{-1}$ in forest. Spearman rank correlations indicated a weak but significant positive relationship between travel-bout duration and speed for CLM3 ($r_s = 0.207$, $p = 7.8 \times 10^{-4}$) and a stronger relationship for CLM4 ($r_s = 0.49$, $p = 1.48 \times 10^{-16}$).

Both CLM3 and CLM4 exhibited movement across all hours of the 24-h cycle. CLM3 showed elevated movement in the early morning (approximately 04:00–08:00), peaking around 06:00, whereas CLM4 displayed a bimodal pattern with peaks in the early morning and late afternoon (16:00–18:00), while maintaining lower levels of movement at other times (Figure 4). Hourly proportions of time spent moving mirrored these patterns, with periods of increased movement corresponding to greater mean distances travelled.



*Co-occurrence at camera stations*

Sunda clouded leopards were detected at 37 of 110 camera stations (34%). Individuals varied in their spatial detection patterns, with some recorded at a single station and others detected at multiple stations (range = 1–12 stations per individual; Table S1). Of the 260 independent detections, 141 (54.2%) were recorded at a single camera station located on Batangan ridge. Across all stations, the number of unique individuals detected per station within each 30- or 60-day window ranged from one to five (two males and three females; Table 5).

At non-Batangan stations, solitary detections predominated. Single-female detections accounted for 57.5% and 61.4% of 30 and 60-day windows, respectively, while single-male detections occurred in 35.0% (30-day) and 28.6% (60-day) of windows. Detection windows involving multiple individuals were uncommon at these sites, with

mixed-sex detections (1 male, 1 female) occurring in 7.5% (30-day) and 4.3% (60-day) of windows.

In contrast, Batangan ridge showed substantially higher frequencies of multi-individual detections. Mixed-sex detections occurred in 35.5% of 30-day windows and 22.2% of 60-day windows. Same-sex male detections (2 males) were recorded in 6.5% (30-day) and 11.1% (60-day) of windows, and detections involving one male and two females occurred in 6.5% and 5.6% of 30- and 60-day windows, respectively. Eight photographic records documented scent-marking behaviour, six of which were recorded at Batangan and involved three different males. The remaining two records occurred at separate stations and involved one male and one female.

### *Temporal activity*

Camera-trap data indicated that both male and female Sunda clouded leopards exhibited cathemeral activity, with detections occurring across all diel periods (Figure 6; Table 6). Activity for both sexes peaked around dawn and declined during the middle of the day. Females showed a secondary activity peak around dusk followed by a gradual decline toward midnight, whereas male activity increased prior to dusk and remained relatively constant throughout the night. These patterns resulted in moderate temporal overlap between sexes ($\Delta_4$ = 0.74, 95% CI: 0.63–0.84; Figure 6).

## Discussion

### *Home range, spatial overlap, and communication*

This study provides the first high-resolution GPS telemetry data describing individual-level movement and space use in Sunda clouded leopards, offering new insight into the spatial ecology of this elusive felid. Our tracking data indicate that adult males in

the Lower Kinabatangan Wildlife Sanctuary occupied home ranges of approximately 41 km² (k-LoCoH), while the single collared female used a substantially smaller area of approximately 7 km². Previously published movement data for this species are limited to a VHF-collared female tracked for 109 days in central Sabah, with estimated ranges of 22.6 km² (95% MCP) and 16.1 km² (95% KDE) (Hearn et al., 2013). The scarcity of comparable telemetry data currently limits direct comparison across landscapes or levels of disturbance, underscoring the value of additional GPS-based studies.

Male home-range sizes observed here are broadly consistent with those reported for mainland clouded leopards (*N. nebulosa*) in Thailand. Grassman et al. (2005) reported 95% KDE ranges of 35.5–43.5 km² for males, while Austin et al. (2007) documented ranges of approximately 40 km² for both sexes using similar estimators. Although such comparisons should be interpreted cautiously given differences in habitat, sampling duration, and analytical methods, they suggest broadly comparable spatial requirements across the two species.



Comparisons among estimators in this study revealed substantial variation in estimated home-range size, with KDE and MCP producing ranges that were several-fold larger than those derived using k-LoCoH and frequently extending into non-forested areas such as oil palm plantations. These differences arise from the underlying properties of the estimators: KDE smooths utilisation distributions across space, and MCP delineates the outermost extent of recorded locations, both of which can incorporate areas not actually used by the animal (Getz et al., 2007). In fragmented landscapes such as the Kinabatangan floodplain, where movement is constrained by habitat boundaries, this can lead to inflated estimates of space use relative to boundary-based approaches such as LoCoH. In contrast, k-LoCoH

estimates more closely reflected observed GPS locations and generally conformed to forest boundaries, consistent with the strong forest association previously documented for this species (Hearn et al., 2018a). Exploratory MCPs derived from camera-trap detections further highlighted the sensitivity of boundary-based estimators to sampling design, with estimates varying widely among individuals and survey periods and often differing markedly from telemetry-derived values. This likely reflects the fact that camera-trap detections represent spatially structured samples of animal movement rather than continuous tracking data.

Patterns of spatial overlap indicated strong segregation among adult males and substantial overlap between sexes. The two tracked males exhibited minimal overlap (~8%), whereas the collared female overlapped extensively with one male and to a lesser extent with the other. Similar patterns have been reported in other solitary felids, where male ranges are largely exclusive and overlap one or more female ranges, reflecting mating systems and resource distribution (Macdonald et al., 2010). Camera-trap data provided complementary support for these patterns, with solitary detections predominating at most sites and mixed-sex detections occurring infrequently outside a single focal area. This is consistent with limited male–male overlap and greater inter-sex overlap inferred from telemetry, while also indicating that individuals converge at specific locations such as Batangan ridge, in some cases at the edges of their home ranges.

In contrast, Batangan ridge emerged as a repeatedly used site visited by multiple individuals of both sexes. GPS data showed that the home ranges of all collared males intersected at this location, and camera-trap records indicated frequent use by additional uncollared individuals. The concentration of mixed- and same-sex detections, together with the majority of observed scent-marking events occurring at

this site, indicates that Batangan functions as a shared-use location facilitating indirect communication. Previous work has demonstrated that Sunda clouded leopards repeatedly use discrete scent-marking sites that are visited by multiple individuals (Allen et al., 2016), supporting the interpretation of these locations as communication hubs. Previous studies have also shown that Sunda clouded leopards preferentially use ridgelines, likely because they facilitate movement across rugged landscapes (Hearn et al., 2018b; Macdonald & Bothwell et al., 2018). Our findings suggest that these patterns may be linked, with ridgelines potentially serving not only as movement corridors but also as focal locations for communication. This interpretation remains speculative and warrants further investigation, but is consistent with the use of spatially discrete communication sites documented in other solitary felids, including Eurasian lynx (*Lynx lynx*) and tigers (*Panthera tigris*) (Smith et al., 1989; Vogt et al., 2014). Notably, visitation rates at Batangan ridge varied over time, suggesting that use of such sites may be dynamic, with individuals potentially selecting or avoiding them depending on social or reproductive context. For example, one adult female (CLF3) was detected with a juvenile during the first survey phase and did not visit Batangan during this period, but was subsequently recorded there repeatedly once the juvenile was no longer observed. This pattern suggests that use of shared sites may vary with reproductive context, potentially reflecting avoidance of conspecific interactions while caring for dependent young. Identifying and targeting such communication sites may improve the efficiency of camera-trap surveys, as demonstrated in other felids such as snow leopards (*P. uncia*) (Krofel et al., 2025).

*Movement patterns and temporal activity*

GPS telemetry revealed that movement in Sunda clouded leopards was characterised by short, frequent travel bouts interspersed with extended stationary periods. Males travelled an average of 3.18–4.12 km per day, with occasional daily movements exceeding 13 km, whereas the collared female exhibited lower daily movement distances. Similar sex-based differences in movement have been reported in other felids and are commonly associated with differences in space-use strategies, energetic demands, and reproductive roles.

Stationary periods occurred almost exclusively within forest habitat, suggesting that Sunda clouded leopards preferentially rest in forested areas. This pattern may reflect avoidance of human activity in oil palm plantations, as well as the structural complexity of forest habitats, which provide understory cover and arboreal resting opportunities for this partially arboreal species. Movements through oil palm plantations and along roads were infrequent for males and were not recorded for the collared female, but when they did occur, males travelled faster in these open or structurally simplified habitats than in forest. This likely reflects more rapid, directed transit through areas perceived as risky, potentially to minimise time spent exposed. Although road mortality of Sunda clouded leopards in Borneo appears to be rare, it has been documented (Nájera et al., 2013; Hearn et al., 2026), and continued expansion of road networks across the island is therefore expected to increase the likelihood of vehicle collisions and associated mortality (Jantz et al., 2025).

Both collared males exhibited activity across the full 24-hour cycle, with individual-specific peaks in movement during early morning and late afternoon periods. Camera-trap data similarly indicated cathemeral activity in both sexes, with pronounced dawn peaks and a secondary dusk peak in females. Thus, the two datasets were broadly consistent in indicating crepuscular peaks within an overall

cathemeral activity pattern, although these peaks appeared sharper in the camera-trap data than in the telemetry data. This difference may partly reflect the smaller telemetry sample size, as well as the concentration of camera-trap detections at Batangan ridge, where temporal patterns may be influenced by repeated visitation to this focal site. Moderate temporal overlap between sexes suggests shared activity windows combined with partial temporal partitioning. Such flexibility in activity patterns is consistent with previous studies of Sunda clouded leopards and may reflect responses to prey activity, environmental conditions, or intraspecific interactions (Ross et al. 2013; Hearn et al. 2018b). The positive relationship between travel-bout duration and movement speed further suggests that longer bouts represent more directed movement, although the behavioural context of these movements cannot be directly inferred from telemetry data alone.

*Conservation implications and future directions*

The large, largely exclusive home ranges observed among males, together with the strong concentration of resting and stationary behaviour within forest habitat, highlight the importance of maintaining landscape-scale connectivity and sufficient contiguous forest to support viable populations. Our results indicate that forested areas are disproportionately important for key behaviours, including resting and prolonged use, whereas oil palm habitats are used primarily for transient movement. This reinforces the conservation value of remaining forest patches within the Kinabatangan floodplain, even where they are degraded or fragmented. Protecting and restoring these forest areas is therefore likely to be critical for the persistence of clouded leopard populations in human-modified landscapes.

This study demonstrates the value of integrating GPS telemetry with camera-trap data to describe fine-scale space use, movement, and site sharing in a cryptic, low-density carnivore within a highly modified landscape. Given the limited number of individuals tracked and the focus on a single landscape, these findings are intended as an individual-level baseline rather than population-level inference. Future studies incorporating additional individuals, longer tracking durations, and comparisons across landscapes of differing connectivity will be essential for refining understanding of Sunda clouded leopard spatial ecology and informing conservation planning.

## Figures, tables and additional files

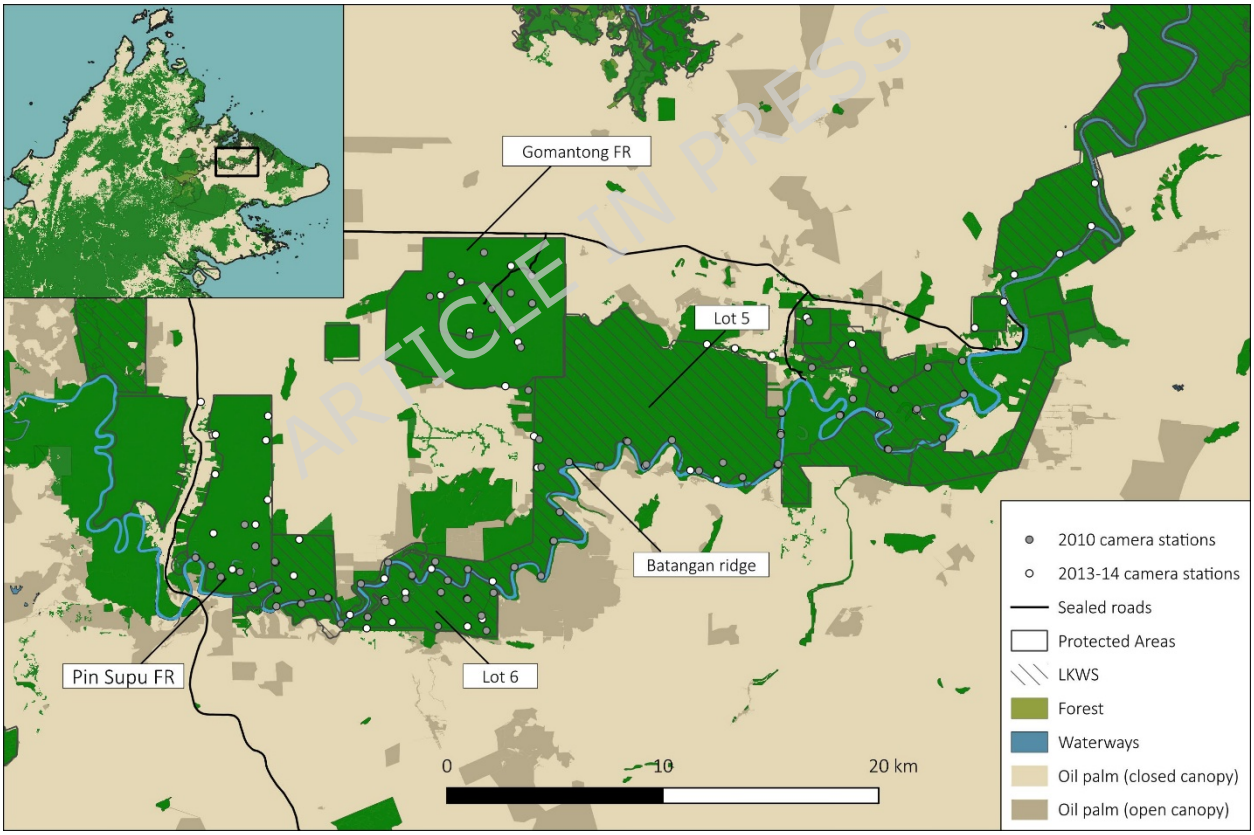


Figure 1. Map of the Lower Kinabatangan floodplain, located in eastern Sabah, Malaysia, showing the locations of camera trap deployments across Lots 5 and 6 of

the Lower Kinabatangan Wildlife Sanctuary (LKWS), and Pin Supu and Gomantong Forest Reserves.

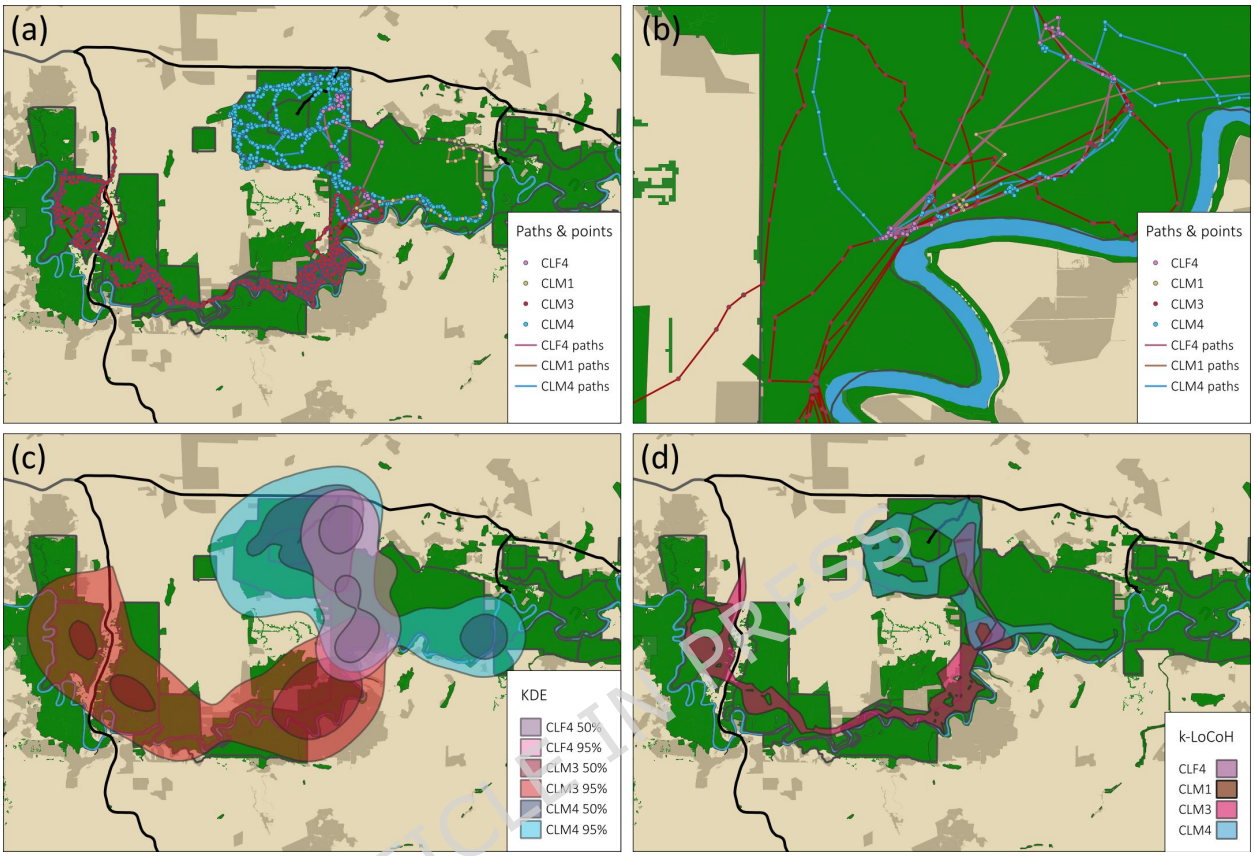


Figure 2. Spatial data of Sunda clouded leopards in the Lower Kinabatangan floodplain, eastern Sabah. Movement paths and recorded locations of GPS-collared individuals across the full study area (a) and in the Batangan ridge focal region (b). Home range estimates generated using the kernel density estimator (c) and k-LoCoH methods (d). For land use descriptions, refer to the Figure 1 legend.

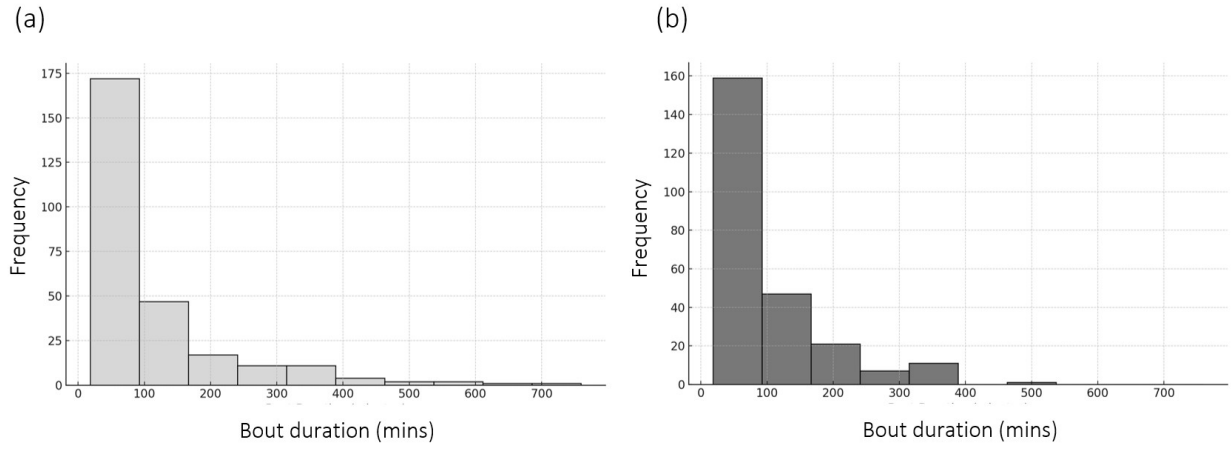


Figure 3. Histograms of Sunda clouded leopard travel bout durations for (a) diurnal (06:00-18:00) and (b) nocturnal (18:01-05:59) periods.

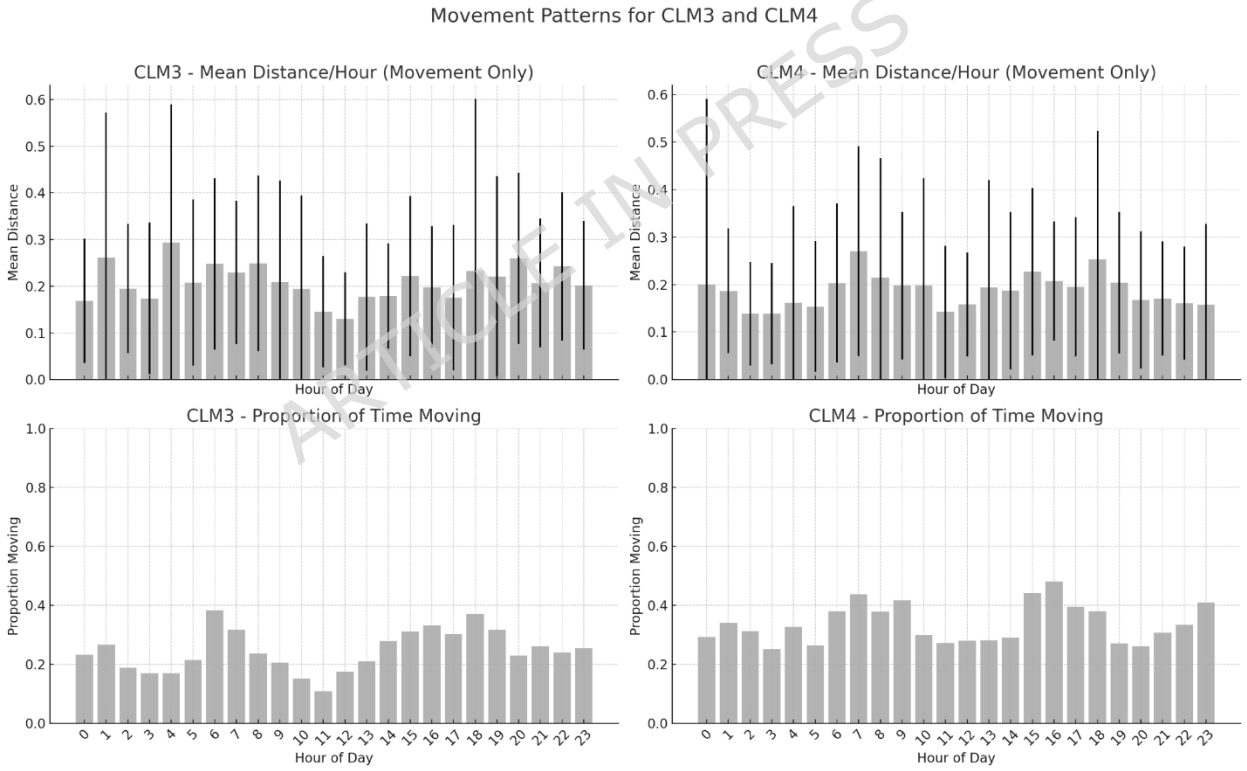


Figure 4. Figure 4. Temporal patterns of movement for two GPS-collared male Sunda clouded leopards (CLM3 and CLM4). Panels show (top) mean distance moved per hour and (bottom) the proportion of time spent moving across the diel cycle.

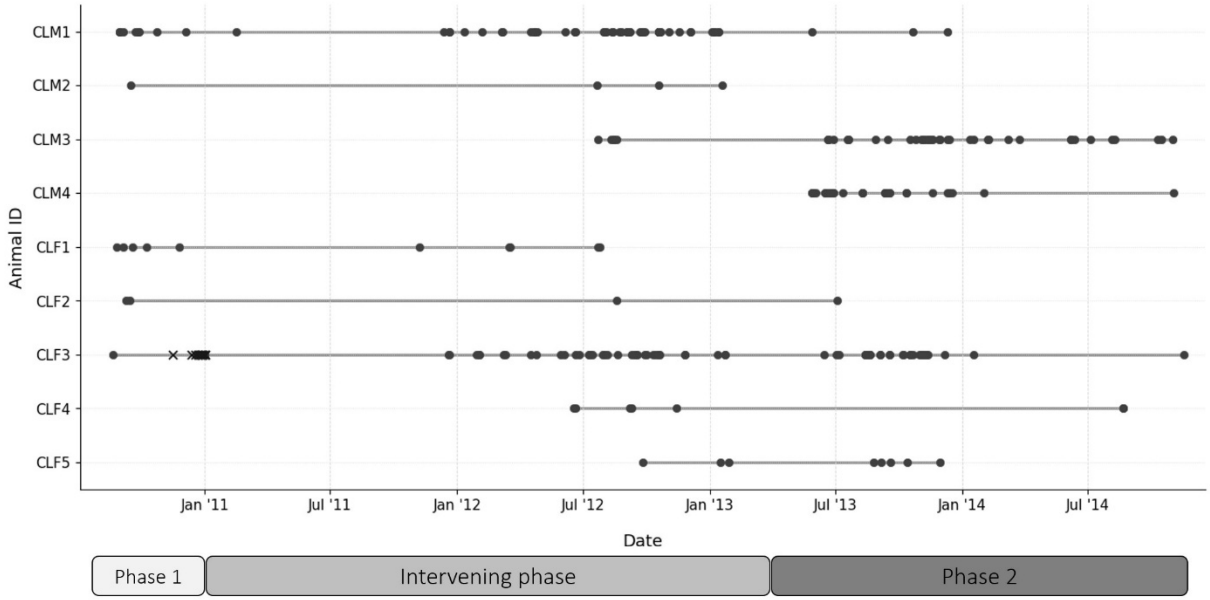


Figure 5. Detection histories of individual Sunda clouded leopards recorded by camera traps between 2010 and 2014. Black dots represent independent photographic detections, with crosses indicating detections of CLF3 with a juvenile. Horizontal lines indicate the temporal span between first and last detections for each individual. Survey phases are shown below the x-axis.

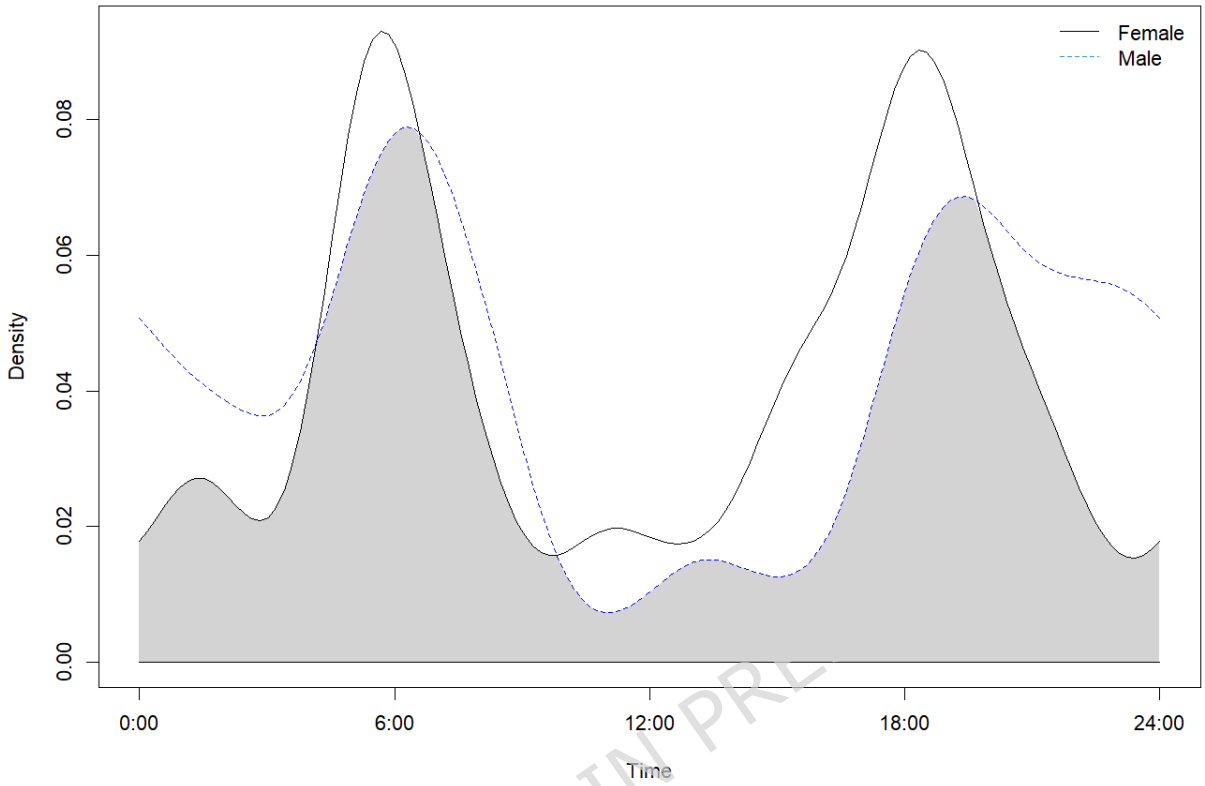


Figure 6. Kernel density estimates illustrating the temporal activity patterns of male and female Sunda clouded leopards in the Lower Kinabatangan floodplain. Estimates are based on detection events recorded by camera traps deployed throughout the study area from 2010-2014 (male: 138 independent records; female: 122 independent records).

*Tables*

Table 1. Telemetry data for four individual Sunda clouded leopards captured and tagged within the Lower Kinabatangan Wildlife Sanctuary, Sabah, Malaysian Borneo, of which three included sufficient data to estimate home range use. DOP: Dilution of precision. k-LoCoH: fixed-k local convex hull range estimator. KUD: Kernel utilisation density. MCP: Minimum convex polygon.

| Animal ID | Sex | Duration of collar data | | No. points (DOP ≤8) | Home range ($km^2$) | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | k-LoCoH | KUD | | MCP | |
| | | Dates | No. days | | | 50% | 95% | 50% | 95% |
| CLM3 | Male | 15/09/2013 - 27/12/2013 | 103 | 5618 | 41.08 | 35.14 | 175.12 | 49.04 | 199.72 |
| CLM4 | Male | 01/02/2014 - 11/3/2014 | 39 | 2498 | 41.79 | 45.68 | 162.84 | 44.58 | 118.71 |
| CLM1 | Male | 22/03/2014 - 27/03/2014 | 6 | 70 | - | - | - | - | - |
| CLF4 | Female | 16/08/2014 - 06/10/2014 | 51 | 158 | 6.98 | 18.71 | 67.77 | 15.55 | 23.08 |

Table 2. Pairwise home range overlap among three GPS-collared Sunda clouded leopards, based on k-LoCoH isopleths. Values represent the absolute area of overlap ($km^2$), and the overlap area as a percentage of each individual's k-LoCoH home range.

| Individual A | Individual B | Home range overlap | | |
|---|---|---|---|---|
| | | Area ($km^2$) | % of A's range | % of B's range |
| CLM3 | CLM4 | 3.5 | 8.4 | 8.3 |
| CLM3 | CLF4 | 1.4 | 3.5 | 20.9 |
| CLM4 | CLF4 | 4.8 | 11.4 | 68.5 |



Table 3. Mean daily distances moved by GPS-collared Sunda clouded leopards in the Lower Kinabatangan, derived using two approaches.

| Animal ID | | Daily distance moved (all GPS points) (km) | | Daily distance moved (consecutive-days) (km) | |
|---|---|---|---|---|---|
| | n | Mean (SD) | Min-max | Mean (SD) | Min-max |
| CLM3 | 96 | 3.18 (3.00) | 0.00 – 13.03 | 2.12 (2.37) | 0.01 – 11.63 |
| CLM4 | 39 | 4.12 (3.23) | 0.08 – 9.72 | 2.62 (2.28) | 0.02 – 9.12 |
| CLM1 | 6 | 4.08 (3.40) | 0.05 – 7.48 | 2.73 (3.02) | 0.05 – 6.44 |
| CLF4 | 16 | 2.08 (2.29) | 0.00 – 6.14 | 1.11 (1.29) | 0.01 – 4.34 |

Table 4. Movement speeds for four Sunda clouded leopards moving through different land use types. n: number of travel bouts within each habitat.

| Habitat | CLM3 | | | CLM4 | | | CLM1 | | | CLF4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | Speed (km/h) | | n | Speed (km/h) | | n | Speed (km/h) | | n | Speed (km/h) | |
| | | Mean (SD) | min-max | | Mean (SD) | min-max | | Mean (SD) | min-max | | Mean (SD) | min-max |
| Forest | 276 | 0.53 (0.28) | 0.01–1.67 | 257 | 0.37 (0.27) | 0.04–1.19 | 9 | 0.29 (0.16) | 0.07–0.57 | 23 | 0.19 (0.17) | 0.01–0.66 |
| Oil palm | 22 | 0.91 (0.56) | 0.09–2.11 | 6 | 1.05 (0.53) | 0.53–1.58 | 1 | 0.51 | – | – | – | – |
| Road crossing | 5 | 1.49 (0.33) | 0.91–1.69 | 3 | 0.68 (0.14) | 0.53–0.82 | – | – | – | – | – | – |

Table 5. Proportional frequency of spatiotemporal overlap among Sunda clouded leopards, by group composition and station type (all camera stations, excluding Batangan, and Batangan), summarized over fixed 30- and 60-day non-overlapping windows. Values reflect the percentage of detection windows (i.e., windows in which at least one clouded leopard was recorded) that included each composition.

| Group Composition | All camera stations, excluding Batangan | | Batangan | |
|---|---|---|---|---|
| | % events (30 days) | % events (60 days) | % events (30 days) | % events (60 days) |
| 1 female | 57.5 | 61.4 | - | - |
| 1 male | 35 | 28.6 | 32.3 | 22.2 |
| 1 male, 1 female | 7.5 | 4.3 | 35.5 | 22.2 |
| 1 male, 2 females | - | 1.4 | 6.5 | 5.6 |
| 2 males | - | 2.9 | 6.5 | 11.1 |
| 2 males, 1 female | - | 1.4 | 9.7 | 22.2 |
| 2 males, 2 females | - | - | 3.2 | - |
| 2 males, 3 females | - | - | 3.2 | 11.1 |
| 3 males | - | - | 3.2 | 5.6 |

Table 6. Proportion of temporal activity density of Sunda clouded leopards during defined diel periods. Values in parentheses represent the percentage contribution of a single hour within each time period to the total activity density. Time periods defined as follows: Dawn (05:00–07:00), Day (07:00–17:00), Dusk (17:00–19:00), and Night (19:00–05:00).

| Sex | No. detections | Probability density mass for time period[a] | | | |
|---|---|---|---|---|---|
| | | Dawn | Day | Dusk | Night |
| Females | 122 | 16.9 (8.4) | 30.2 (3.0) | 16.7 (8.3) | 34.8 (3.5) |
| Males | 137 | 14.9 (7.4) | 22.5 (2.3) | 10.6 (5.3) | 51.4 (5.1) |

Supplemental Table S1

| Animal ID | Phase 1 | | | Intervening phase | | | Phase 2 | | |
|---|---|---|---|---|---|---|---|---|---|
| | No. detections | No. camera stations | MCP (100%) | No. detections | No. camera stations | MCP (100%) | No. detections | No. camera stations | MCP (100%) |
| CLF1 | 5 | 5 | 10.0 | 5 | 4 | 12.4 | - | - | - |
| CLF2 | 2 | 2 | 4.7 | 1 | 1 | NA | 1 | 1 | na |
| CLF3 | 15 | 5 | 1.2 | 40 | 9 | 22.9 | 36 | 9 | 57.1 |
| CLF4 | - | - | - | 5 | 1 | NA | 2 | 1 | na |
| CLF5 | - | - | - | 3 | 3 | 2.0 | 5 | 3 | 0.2 |
| CLM1 | 8 | 3 | 21.0 | 48 | 5 | 12.8 | 3 | 2 | NA |
| CLM2 | 1 | 1 | NA | 3 | 2 | NA | - | - | - |
| CLM3 | - | - | - | 5 | 3 | 1.2 | 39 | 12 | 43.1 |
| CLM4 | - | - | - | - | - | - | 29 | 2 | na |
| Unknown | - | - | - | 4 | 4 | NA | 4 | 4 | na |

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## Declarations

*Ethics approval and consent to participate*

Approval for research was granted by the Sabah Biodiversity Centre, Sabah Wildlife Department and Sabah Forestry Department. All trapping and animal handling procedures followed protocols developed jointly by our research team and the Sabah Wildlife Department and were reviewed by the University Complutense's Committee on Animal Care (Department of Animal Physiology, Faculty of Veterinary Medicine; Permit reference number: BVP/PLI/12011/CDAUN0414812/1).

### *Consent for publication*

Not applicable.

### *Availability of data and materials*

Due to the sensitive nature of the data and in order to protect this threatened species, we are unable to share the raw GPS location data underpinning this study. However, derived datasets and supporting information are available for scholarly use upon reasonable request. Interested researchers may obtain access by contacting the corresponding author.



### *Competing interests*

The authors declare that they have no competing interests

### *Funding*

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*Authors' contributions*

AJH: Conceptualization (lead); data curation (equal); formal analysis (lead); Funding acquisition (equal); investigation (equal); supervision (equal); writing – original draft (lead); writing – review and editing (lead). FN: Data curation (equal); Funding acquisition (equal); investigation (equal); writing – review and editing (supporting). GB: Data curation (equal); investigation (equal); writing – review and editing (supporting). MNE: data curation (equal); investigation (equal); writing – review and editing (supporting). SL: formal analysis (supporting); writing – review and editing (supporting). SWT: data curation (equal); investigation (equal); writing – review and editing (supporting). SGS: investigation (equal); writing – review and editing (supporting). NKA: writing – review and editing (supporting). SAB: writing – review and editing (supporting). DWM: Funding acquisition (equal); supervision (equal); writing – review and editing (supporting). BG: Funding acquisition (equal); supervision (equal); writing – review and editing (supporting)



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