Responses of Sunda clouded leopard population density to anthropogenic disturbance and refining estimates of their conservation status in Sabah

Andrew J. Hearn[1*], Joanna Ross[1], Henry Bernard[2], Soffian A. Bakar[3], Benoit Goossens[3,4,5,6], Luke T.B. Hunter[7] and David W. Macdonald[1]

[1] Wildlife Conservation Research Unit (WildCRU), Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney, UK.

[2] Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia

[3] Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

[4] Danau Girang Field Centre, c/o Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia.

[5] Organisms and Environment Division, School of Biosciences, Cardiff University, Cardiff, United Kingdom.

[6] Sustainable Places Research Institute, Cardiff University, Cardiff, United Kingdom.

[7] Panthera, New York, NY, USA

[*] Corresponding author

Keywords: Sunda clouded leopard; *Neofelis diardi*; selective logging, forest management; population density; spatially explicit capture recapture

Word count: 6390

Abstract

Extensive areas of the world's tropical forests have been, and continue to be, disturbed as a result of selective timber extraction. While such anthropogenic disturbance typically results in the loss of biodiversity, many species persist, and their conservation in production landscapes could be enhanced by a greater understanding of how biodiversity responds to forest management practices. We conducted intensive camera trap surveys of eight protected forest areas in Sabah, Malaysian Borneo, and developed estimates of Sunda clouded leopard population density from spatially explicit capture-recapture analyses of detection data to investigate how their abundance varies across the landscape and in response to anthropogenic disturbance. Estimates of population density from six forest areas ranged from 1.39 to 3.10 individuals per 100 km^2. Our study provides the first evidence that Sunda clouded leopard population density is negatively impacted by hunting pressure and forest fragmentation, and that among selectively logged forests, time since logging is positively associated with abundance. We argue that these negative anthropogenic impacts could be mitigated with improved logging practices, such as by reducing the access of poachers by effective gating and destruction of road access points, and by the deployment of anti-poaching patrols. By calculating a weighted mean population density estimate from estimates developed in this paper and from the literature, and by extrapolating this value to an estimate of current available habitat, we estimated there are 754 (95% posterior Interval 325–1337) Sunda clouded leopard individuals in Sabah.

Introduction

While still containing some of the largest contiguous tracts of forested land in Southeast Asia, the rainforests of Borneo are experiencing amongst the highest global levels of forest degradation and loss, principally as a result of selective timber extraction and subsequent conversion to oil palm, *Elaeis guineensis*, plantations (Gaveau et al., 2014, 2016; Cushman et al., 2017). The intricate ecological responses to selective logging of Borneo's forests remain unclear for most species, yet several studies have indicated that many can persist after such management, with only a minority of species studied so far exhibiting markedly reduced post logging densities (e.g., Meijaard et al., 2005; Costantini et al., 2016). In comparison, the conversion of these forests to oil palm production has been shown to result in a very substantial reduction in biodiversity and functional diversity (Fitzherbert et al., 2008; Yue et al., 2015), a pattern mirrored region-wide (Wilcove et al., 2013). Thus, while logged forest undoubtedly has lower intrinsic value to biodiversity conservation than pristine forest, it is becoming increasingly clear that further gains to conservation could be achieved if management of production forests was improved to minimise negative impacts on biodiversity (Meijaard and Scheil, 2008). However, such an optimisation approach, based on an understanding of how biodiversity responds to forest management practices and other anthropogenic disturbances, is currently lacking for many species, and remedying this knowledge gap remains a priority.

The Sunda clouded leopard *Neofelis diardi*, is a medium-sized felid, endemic to the islands of Borneo - where it is the terrestrial apex predator - and Sumatra. This species is currently listed as Vulnerable on the IUCN Red List as a result of a presumed small and declining population size (Hearn et al., 2016a). Assessment of its conservation status and development of effective conservation actions, however, are hindered by a lack of understanding regarding their abundance, distribution and responses to anthropogenic disturbance (Hearn et al., 2016b). Records of Sunda clouded leopards inhabiting a diverse range of forest types, including both pristine and selectively logged forests (e.g., Brodie & Giordano, 2012; Wilting et al., 2012; Cheyne et al., 2013, 2016; Sollmann et al., 2014; McCarthy et al., 2015; Hearn et al., 2016a), indicate that they exhibit some capacity to tolerate anthropogenic disturbance. Brodie et al. (2015a), however, showed that Sunda clouded leopard local scale abundance was lower in logged forest sites compared to unlogged sites. In addition, the movements of Sunda clouded leopards from a fragmented landscape were shown to be positively and strongly associated with forest, including highly disturbed forest types, but negatively associated with a range of non-forest vegetation (Hearn, 2016), thus confirming earlier predictions that forest loss and conversion to oil palm plantations present one of this felid's greatest threats (Rabinowitz et al., 1987; Hearn et al., 2016a,b). Indeed, the increasing prevalence of vast tracts of oil palm plantations throughout this species' range is likely resulting in the fragmentation of habitat and the consequent isolation of individual populations, potentially making them increasingly vulnerable to demographic stochastic processes and inbreeding depression. Robust spatial ecology data are lacking for the Sunda clouded leopard, but preliminary analyses suggest that they have relatively large home ranges (Hearn et al., 2013). It is thus conceivable that as forests become increasingly fragmented, and forest patches decline in size, they become less able to support viable populations, resulting in reduced population densities, and, ultimately, local extirpation.

While recent research has provided new insights into how anthropogenic pressures influence Sunda clouded leopard abundance and habitat selection at a local scale, how these responses translate into changes to their population density remains unknown. Sollmann et al. (2014) estimated that Sunda clouded leopard density from two primary and two mixed forest (primary and secondary) areas in Sumatra ranged from around 0.8 to 1.6 individuals per 100 km², but found no statistical support for differences in density between the populations. In the Malaysian state of Sabah, northern Borneo, Brodie & Giordano (2012) estimated that Sunda clouded leopard density from an area of primary forest was 1.9 individuals per 100 km^2, whereas Wilting et al. (2012) presented densities from two selectively logged forests of around 0.8 and 1.0 individuals per 100 km^2. However, akin with Sollmann et al. (2014), the relatively large, overlapping variances of the Sabah-derived estimates suggest that the population densities were not significantly different. Such low precision estimates are a reflection of the difficulty of obtaining sufficiently large sample sizes. This is typical of studies of elusive forest felids (Foster & Harmsen, 2012) and hinders our ability to draw robust conclusions regarding the Sunda clouded leopard's responses to disturbance, potentially masking any underlying problems.

As obligate carnivores, large felid abundance is directly affected by prey density under a wide range of ecological conditions (Carbone & Gittleman, 2002; Karanth et al., 2004), and so it is reasonable to assume that prey densities are a key limiting factor for Sunda clouded leopards. Quantitative data regarding Sunda clouded leopard diet preferences are lacking, but incidental reports and observations from Borneo (e.g., Rabinowitz et al., 1987; Yeager, 1991; Matsuda et al., 2008) suggest that they exploit a diverse array of mammals, and studies of temporal activity overlaps and patterns of co-occurrence with potential prey (Ross et al., 2013) indicate that ungulates may be a key resource. Thus, the response of Sunda clouded leopards to anthropogenic disturbance may be mediated largely by the responses of their prey to such habitat modification. Bornean mammalian responses to selective logging vary greatly, but their sensitivity to disturbance is positively correlated with their phylogenetic age and dietary specificity, and negatively correlated with their ecological niche width (Meijaard & Sheil, 2008; Meijaard et al., 2008). Brodie et al. (2015a) showed that, compared to estimates in unlogged forest, muntjac (*Muntiacus* spp.) and mousedeer (*Tragulus* spp.) abundance declined, and bearded pig (*Sus barbatus*) and sambar deer (*Rusa unicolor*) increased in old logged forests. The abundance of all four ungulates was lower in recently logged forests. An increased abundance of some species in logged forest may benefit the Sunda clouded leopard and result in elevated abundances compared to primary forest. Conversely, the dense network of logging roads and skids present in production forests permit greater access and thus hunting opportunities for poachers (Laurance et al., 2009), of which ungulates are a favoured quarry (Corlett, 2007). In this balance, increased exploitative competition with humans in selectively logged forests without adequate protection against such threats could result in reduced Sunda clouded leopard densities.

Here, we develop estimates of Sunda clouded leopard population density using spatially explicit capture-recapture analyses of camera trap data from multiple forest areas in Sabah to investigate how density varies across the landscape and in response to anthropogenic disturbance. We test our *a-priori* hypotheses that Sunda clouded leopard population density will be lower in forests with (i) higher hunting pressure and (ii) higher levels of forest fragmentation. We also hypothesise that (iii) among selectively logged forests, time since logging will be positively associated with Sunda clouded leopard density. We combine our results with those from previously published studies to develop an estimate of Sunda clouded leopard population size in Sabah.

Study Areas

Between May 2007 and December 2013, we conducted intensive, systematic camera trap surveys of eight protected forest areas in the Malaysian state of Sabah, northern Borneo (Fig 1, Table 1). We selected survey areas that provided a broadly representative sample of the spectrum of forest types, elevations, anthropogenic disturbance and fragmentation present in the state. We surveyed three primary forests, including one predominantly lowland hill (Danum Valley Conservation Area: Danum Valley), and two largely hill dipterocarp and submontane forests (Tawau Hills Park (Tawau) and Crocker Range Park (Crocker)). We surveyed five forest areas that had been exposed to selective logging, including the Lower Kinabatangan Wildlife Sanctuary (Kinabatangan), Tabin Wildlife Reserve (Tabin), and Kabili-Sepilok, Malua and Ulu Segama Forest Reserves.

Methods

Camera survey protocol

We undertook camera trap surveys designed specifically to estimate Bornean felid population density (Hearn et al., 2016c). Depending on logistical constraints, we deployed cameras according to one of two protocols, applying either a split-grid approach, where the entire grid is sequentially surveyed in two halves, or a simultaneous approach, where all camera stations are deployed in a single phase (Table 2). We deployed cameras primarily along established and newly cut human trails and ridgelines, and occasionally along old, unsealed logging roads, particularly in two of the selectively logged sites (Malua and Ulu Segama; Table 2). Camera stations were spaced approximately 1.5–2.0 km apart, to balance the need for a sufficiently large sampling grid with the need to ensure that each animal's homerange contains several stations (e.g., Foster & Harmsen, 2012). Cameras were positioned around 40–50 cm above the ground and arranged in pairs to enable both flanks of the animal to be photographed simultaneously, to facilitate individual identification.

Assessment of poaching pressure

We followed the approach of Brodie et al. (2015a) and analysed our camera trap data to provide an estimate of poaching pressure for each study area and to enable comparison with estimates of poaching pressure recorded in their previous studies. Our assessment was based on the photographic encounter rate of presumed poachers, calculated as the mean proportion of days that ≥1 poacher was recorded at each camera station. Hunting of birds or mammals of any species is prohibited by law in all our study areas, and people did not live in, or use the forest for any legal purpose other than limited tourism, research and forest management at any of our sites. Excluding obvious records of unarmed park staff, field personnel and tourists, we assumed that any person photographed within the forest was a poacher. In most (86%) cases, people in the forest illegally were photographed carrying shotguns or spears, and/or accompanied by dogs. This approach does not permit assessment of historical poaching pressure, which may arguably be a more important parameter to measure, but does provide a useful, non-subjective assessment of current poaching levels.

SECR analyses

We developed estimates of Sunda clouded leopard population density using a Spatially Explicit Capture Recapture (SECR) approach (Efford, 2004; Royle & Young, 2008), undertaken within a Bayesian framework (Royale et al., 2009). We used the R (version 3.1.2; R Development Team, 2014) package SPACECAP (version 1.1.0; Gopalaswamy et al., 2012) to conduct all SECR analyses. We used pelage markings and morphology to identify and sex individual animals and developed a unique capture history for each animal. Detections of cubs were recorded but only adult animals were included in the analysis. While it has been shown that gender can affect detection parameters in felids, and inclusion of sex as a covariate can consequently improve parameter estimation precision (e.g. Sollmann et al., 2011), we were unable to model sex-specific detection parameters because of the low number of female recaptures and so data for both sexes were pooled and analysed together. We assigned each 24-hour period as a unique sampling occasion, as short sampling interval lengths may improve model precision (Goldberg et al., 2015). We limited our sampling duration to 90 days, apart from one site (Tabin), where the lengthy transition period, and consequent reduction in camera trapping effort, necessitated a period of 120 days to provide sufficient detection frequencies. Such sampling durations are in-line with similar studies to approximate population closure (e.g., Royle et al., 2011; Wilting et al., 2012).

We developed a state space, a polygon defined by the addition of a buffer to the outermost coordinates of each trapping grid, within which we established potential home range centres by delineating a grid of regularly spaced points, with a mesh size of 0.25 km^2. Following Gopalaswamy et al. (2012) we eliminated potential home-range centres from areas predicted to be unsuitable for Sunda clouded leopards using a GIS (ArcMap 10.2, ESRI, Redlands, California, USA) in conjunction with habitat data derived from field knowledge and hi-resolution aerial images from Google Earth (Images: DigitalGlobe). We assumed that Sunda clouded leopards are restricted to forest cover and not found in oil palm plantations (Hearn et al., 2016b) and so we considered forested areas (both pristine and disturbed) as habitat and all other non-forest land uses, as unsuitable. During a sequence of preliminary runs, we systematically increased buffer size until the probability of detection at the state space boundary was negligible. Accordingly, buffer size varied from 12 to 30 km.

We ran all SPACECAP density estimation analyses using a half normal detection and Bernoulli's encounter model, with 100,000 Markov-Chain Monte Carlo (MCMC) iterations and a thinning rate of 1. We varied burn-in for each survey until adequate parameter convergence was attained, which we assessed by means of Geweke tests; z scores falling between -1.64 and 1.64 were deemed acceptable. Program SPACECAP applies a data augmentation process in which a theoretical population of zero-encounter history individuals is added to the dataset of known animals (Gopalaswamy et al., 2012). We varied data augmentation values for each survey, assigning a final value following a series of preliminary runs, increasing data augmentation where necessary to ensure that ψ, the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value, did not exceed 0.8. Finally, we examined the Bayesian *p*-value provided by program SPACECAP, which measures the discrepancy between observed data and expected values, to assess the goodness-of-fit of the model; models presenting *p*-values of around either 0 or 1 were considered inadequate (Gelman et al., 1996; Gopalaswamy et al., 2012). For each parameter estimated, we present the posterior mean, standard deviation, and 95% Bayesian highest posterior density (HPD) interval. The HPD is the shortest interval enclosing 95% of the posterior distribution. Following Sollmann et al. (2014) we consider parameters from each site to be significantly different if the 95% HPD of one does not include the mean of the other.

Estimation of population size in Sabah

We developed an estimate of Sunda clouded leopard population size for Sabah based on extrapolation of an estimate of this species' density to an estimate of current available habitat. Following a meta-analysis approach, we calculated a weighted mean population density estimate from estimates developed in this paper (n=6) and from previous published estimates from Sabah (Brodie and Giordano, 2012, n=1; Wilting et al., 2012; n=2), by weighting each unique value by the inverse of their coefficient of variation, based on their respective 95% HPD values. Using the same weighted approach, we calculated a mean upper and lower density estimate, based on each value's upper and lower quantiles. For an approximation of available Sunda clouded leopard habitat, we assumed that these felids are restricted to forest habitats and used an estimate of Sabah forest cover for the year 2015 developed by Gaveau et al. (2016), based on analysis of LANDSAT imagery. Gaveau et al.'s (2016) definition of forest included closed-canopy, old-growth and selectively logged dipterocarp, heath, fresh-water and peat swamp forests and mangrove forests, but excluded young forest regrowth, scrublands, tree plantations, agricultural land, and non-vegetated areas, and thus closely matches current predictions for clouded leopard habitat associations (Hearn et al., 2016b). It is important to note that this definition of available habitat includes forest types from which no robust density estimates are currently available (i.e., heath forests, peat swamp forests and mangrove), and so our population estimate should be treated with appropriate caution.

Results

Photographic capture success

We recorded 528 independent photographic captures of Sunda clouded leopards, with records stemming from all survey areas apart from Kabili-Sepilok (Table 2). We found evidence of breeding activity at three sites, recording two different cubs in Crocker and one in both Malua and Tawau (Table 2). The number of independent photographic captures within the closed survey period varied greatly across the different sites, ranging from 10 to 101 (mean = 41), and the number of different individual animals recorded within this period ranged from 5 to 10 (Table 3). We could assign individual identity to all but one of the photographic captures, a female from Malua. At most sites, we recorded more individual males than females, and males typically had higher recapture rates than did females (Table 3).

Assessment of poaching pressure

We found evidence of probable poaching activity in all forest areas, apart from Danum (Table 4). The lowest poacher detection rates were found in Danum, Ulu Segama and Tawau, where camera theft was also low, and the highest in Kinabatangan and Malua, where camera theft was high. Camera theft from Crocker was also relatively high. Tabin had a relatively high poacher detection rate but a relatively low incidence of camera theft.

Density estimates

We developed estimates of Sunda clouded leopard density at all study sites at which they were detected apart from Malua, in which low numbers of photographic captures prevented SECR model convergence, and so was removed from subsequent analyses. At all other sites Bayesian *p*-values indicated that the models were of an adequate fit (Table 5) and Geweke tests indicated that all model parameters converged. Sunda clouded leopard density across these six sites varied from 1.39 to 3.10 individuals per 100 km^2 (Table 5). The two highest density estimates stemmed from the enrichment-planted Ulu Segama (3.10 individuals per 100 km^2 ± SD 1.11) and selectively logged Tabin (2.66 ± SD 1.11), and the lowest from the primary upland Crocker (1.39 ± SD 0.41) and the highly degraded and fragmented Kinabatangan (1.54 ± SD 0.70). Sunda clouded leopard density was significantly higher in Ulu Segama than Crocker, Danum and Kinabatangan, and density in Tabin was significantly higher than in Crocker and Kinabatangan, but we otherwise found no statistical support for differences in density between any other sites. The movement parameters from Kinabatangan and Tabin were significantly larger than that from all other sites, and the estimate from Kinabatangan was significantly larger than that from Tabin, by almost a factor of two (Table 5).

Estimation of population size in Sabah

The weighted mean population density developed from nine available density estimates was 1.90 individuals per 100 km^2, and the weighted lower and upper 95% posterior intervals were 0.82 and 3.37 individuals per 100 km^2, respectively. Based on data derived from Gaveau et al. (2016), the amount of available habitat in Sabah in 2015 was 39,693 km^2. Extrapolation of the weighted density estimate to this habitat assessment produced an estimated population size of 754 (95% posterior interval 325–1337) individuals for Sabah.

Discussion

Influence of anthropogenic disturbance on Sunda clouded leopard density

We present estimates of Sunda clouded leopard population density from six of eight forest areas we surveyed in Sabah, Borneo, including the first for this species from enrichment-planted, highly fragmented, and submontane forest types. Our estimates of density from forest areas exposed to varying levels of anthropogenic disturbance ranged from 1.39 to 3.10 individuals per 100 km^2, and are thus comparable with those from previous studies in Sabah (0.84–1.9: Brodie and Giordano, 2012; Wilting et al., 2012), the Indonesian province of Central Kalimantan (0.72–4.41: Cheyne et al., 2013) and Sumatra (0.8–1.6: Sollmann et al., 2014). Nevertheless, statistically significant differences in Sunda clouded leopard population density were evident between several of our study areas.

While the absence of replication in our study approach limits our ability to draw robust conclusions about the possible influence of anthropogenic disturbance on Sunda clouded leopard densities, our results support our first *a-priori* hypothesis that population density is negatively impacted by poaching pressure. Indeed, the two areas with the lowest estimates, the primary uplands of the Crocker Range Park and the low lying logged forests of the Lower Kinabatangan, were subject to some of the highest levels of poaching pressure, whereas forest areas with a relatively low incidence of poaching, e.g., Danum Valley, Ulu Segama and Tawau, yielded some of the highest densities. In the case of Ulu Segama, the estimate of density was statistically higher than that of the two lowest density sites. It is worth noting that the comparatively low density found in Crocker Range may also be a reflection of higher elevation forest supporting lower productivity. While we are unable to disentangle the possible influence of low detection probabilities as a result of other factors unrelated to abundance (Sollmann et al., 2013), the very low photographic capture success from Malua Forest Reserve, where poaching intensity was the highest of our study areas, is indicative of a low population density relative to our other sites. The high density estimate from Tabin Wildlife Reserve, which was also significantly higher than that of our two lowest density sites, yet was subject to moderate levels of poaching, appears to contradict this trend. However, unlike other areas where poaching activity was more diffuse, most records of poaching activity in Tabin typically involved poachers spot-lighting from four-wheel-drive vehicles along the single access road within the reserve, or occasionally along the western border with an oil palm plantation. It is, therefore, possible that the impact of poaching was not widespread throughout the study area.

Our data also tentatively support our second *a-priori* hypothesis that Sunda clouded leopard population density will be lower in forests with higher levels of forest fragmentation. Firstly, the Lower Kinabatangan, which is composed of several relatively small forest patches embedded within a largely oil palm plantation landscape, supported the second to lowest density of all our areas. Secondly, we found no evidence of Sunda clouded leopards within the Kabili-Sepilok Forest Reserve, a small (42.76 km^2), potentially isolated dipterocarp forest fragment contiguous with a coastal chain of mangrove and nipah palm, but otherwise surrounded by oil palm plantations. Forestry Department staff stationed in the area report that the species had been recorded there in the past, so it is likely that gradual loss of surrounding forest and conversion to oil palm plantations has led to local extirpation. Kabili-Sepilok Forest Reserve is a probable harbinger of the effects of ongoing fragmentation which will be detrimental to Sunda clouded leopard populations across much of its remaining range.

The low number of photographic captures from Malua Forest Reserve, which was surveyed just one year after selective logging operations ceased, provides tentative support for our third *a-priori* hypothesis, that time since logging is positively related to Sunda clouded leopard density in selectively logged forests. Furthermore, our two highest density estimates stemmed from two forests surveyed 16 and 20 years post logging activities, of which one, the enrichment-planted Ulu Segama Forest Reserve, was statistically higher than that from the primary Danum Valley Conservation Area. It is noteworthy that Wilting et al's (2012) survey of the Tangkulap-Pinangah Forest Reserve in Sabah, just eight years after logging operations stopped, yielded a density of 0.84 individuals per 100 km^2, which is lower than any of our estimates. Brodie et al. (2015a) showed that, compared to unlogged forest areas, the abundance of four ungulate species was lower in recently logged areas, whereas bearded pig and sambar deer were more abundant, and muntjac and mousedeer less abundant in old logged areas. Thus, while we cannot be sure by what mechanism the effect may operate, one hypothesis is that following recent logging there is a direct negative effect on prey abundance and or availability, which declines over time. Another, not mutually exclusive, hypothesis is that the logging operations, and associated proliferation of roads, increases both the number of poachers and their penetration of the forest, reducing prey populations and perhaps also inflicting a by-catch on the Sunda clouded leopards themselves, and that the relative impact of these roads diminishes over time as the roads become unnavigable. Brodie et al. (2015b) found that an increase in road density on Borneo is associated with reduced local occurrence of Sunda clouded leopards, and in Sumatra, Haidir et al. (2013) found that this felid's habitat use was positively affected by distance to forest edge. In another Sumatran study, McCarthy et al. (2015) reported that this species occurred most commonly at moderate distances from roads, rivers and forest edges, all features which assist the movement of people.

Our results confirm earlier suggestions (e.g., Wilting et al., 2006; Hearn et al., 2016a,b) that selectively logged forest provides an important resource for Sunda clouded leopards, and suggests that appropriate management of these commercial forests could further enhance their conservation value. Our results suggest that the overriding priority is to reduce poaching pressure, both on these felids and their prey, by reducing access to the forest interior along logging roads. Reduction of vehicular access could be achieved through the installation of gates and the destruction of bridges following the cessation of logging activities. This is particularly important in more recently logged forests, which will have a more extensive network of gravel roads that are still passable. Such efforts will not prevent access on foot, and so measures such as anti-poaching patrols, while expensive, are also an essential tool to reduce the threat from poaching in these forests.

Estimation of population size in Sabah

We provide the first estimate of Sunda clouded leopard population size for the Malaysian state of Sabah based on robust spatially explicit capture recapture density estimates from nine forest areas within the state. Our estimated population size of around 754 (95% posterior interval 327–1337) individuals is a significant methodological improvement on the very approximate estimate of 1500–3200 individuals provided by Wilting et al. (2006), based on extrapolation of a track-based assessment of density from Tabin Wildlife Reserve. Our basic model of population size does not include a minimum patch size or measure of proximity to other patches in its calculation, as such data are currently lacking. Nevertheless, their apparent absence from the relatively small forest fragment of Kabili-Sepilok suggests that our estimate of available habitat may be slightly inflated, and with it our population estimate. In addition, while we made efforts to survey a range of forest types and levels of anthropogenic disturbance, there are a number of forest types that were not included. Of these, mangrove forest, given its potential importance in connecting otherwise isolated populations, is particularly important. Surveys within these habitats and efforts to determine minimum patch sizes for this felid are therefore a priority.

As forest cover on Borneo declines, there is an increasing need to assess the population size of this felid across the entire island, and thus the conservation status of the Bornean sub species, *Neofelis diardi* ssp. *borneensis*. The Sabah bias of our data, and the lack of robust spatially explicit density estimates from outside this region currently hinders such assessment. While the overall nature of the forests within Sabah broadly parallels those of the island as a whole, outside of this state there are stark differences in forest management and patterns of deforestation (Cushman et al., 2017). Furthermore, the threat from hunting and/or poaching, which we have shown to be a potentially important factor influencing Sunda clouded leopard density, is likely to vary considerably throughout the island. There is increasing evidence that Sabah's forests have hitherto been subjected to lower influences of hunting and poaching than elsewhere and that populations densities may be far lower outside of this region. Indeed, the mean encounter rate of hunters/poachers from five areas in Sarawak were more than an order of magnitude higher than that described in this paper (Brodie et al., 2015a). Furthermore, Cheyne et al. (2016) surveyed eight forest areas in Kalimantan with a comparable effort and approach to that used in our study, and recorded an exceptionally low number of Sunda clouded leopard records (≤3) from each of six of these forests, which could be indicative of low population densities. Efforts should thus be made both to establish the incidence of poaching across this felid's range, and to derive robust, spatially explicit estimates of their density outside of Sabah to help better inform the conservation of this elusive wild cat.

Acknowledgements

We are indebted to our research assistants, especially Gilmoore Bolongon. We offer thanks to Glen Reynolds and the Royal Society's SEARRP for logistical support, and Rahel Sollmann and Paul Johnson for statistical advice. We thank Sabah Parks, Sabah Forestry Department, Sabah Wildlife Department, Yayasan Sabah, the State Secretary, the Sabah Chief Minister's Department, and the Sabah Biodiversity Centre for permission to conduct research. This research was primarily funded by the Darwin Initiative, Recanati-Kaplan Foundation, Robertson Foundation, and Sime Darby Foundation, with additional funding from Clouded Leopard Project, Felidae Conservation Fund, Houston Zoo, HG Wills International Trust for Nature Conservation, Panthera, Point Defiance Zoo and Aquarium and Wild About Cats.

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Biographical sketches

ANDREW J. HEARN's interests lie in the distribution, status, spatial ecology, and conservation of the guild of sympatric felids on Borneo. JOANNA ROSS's research focuses on the ecology and conservation of members of the Bornean felid guild and other threatened Bornean Mammals. HENRY BERNARD has research interests in Bornean small mammal communities and proboscis monkeys. SOFFIAN A. BAKAR's core interests lie in the conservation and sustainable management of wildlife in Sabah. BENOIT GOOSSENS is Director of the Danau Girang Field Centre in Sabah where he is running long-term programmes on an array of tropical forest species to understand their biological responses to rainforest fragmentation and oil palm monoculture. LUKE HUNTER oversees the direction and strategy of Panthera's global wild cat conservation programs. DAVID W. MACDONALD has a background in behavioural ecology, with an emphasis on carnivores.

Table 1. Details of the eight forest study areas in Sabah, Malaysian Borneo. Study areas are arranged in approximate order of increasing disturbance (level of fragmentation and exposure to selective logging practices).

Study area	Location (Lat/ Lon)	Size (km^2) [a]	Level of isolation /fragmentation of forest patch	Dominant landcover type(s) / logging exposure	Time since logging (Years)
Danum Valley	4° 58' N, 117° 46' E	438	Low. Part of ca. 1 million ha Central Sabah Forest complex	Primary, lowland & hill dipterocarp.	N/A
Tawau	4° 27' N, 117° 57' E	280	Medium. Large, relatively isolated forest block, contiguous with commercial Forest Reserve to North.	Primary, lowland & hill dipterocarp, sub-montane & montane.	N/A
Crocker	5° 26' N, 116° 02' E	1399	Medium. Large, relatively isolated forest block.	Primary, hill dipterocarp, sub-montane & montane.	N/A

Ulu Segama	4° 59’ N, 117° 52’ E	2029	Low. Part of ca. 1 million ha Central Sabah Forest complex	Selectively logged (1978-1991), lowland Dipterocarp. Medium density of open and semi-closed logging roads. Enrichment planted in 1993.	16
Tabin	5° 14’ N, 118° 51’ E	1,205	Medium. Large, relatively isolated forest block. Possible connectivity with coastal mangrove to North.	Selectively logged (1969-1989), lowland dipterocarp. Low density of open and semi-closed logging roads.	20
Kabili-Sepilok	5° 51’ N, 117° 57’ E	42.9	High. Small, isolated fragment. Possible connectivity along coastal mangrove system	Partially selectively logged (low impact, ceased 1957), lowland Dipterocarp, heath forest & mangrove.	>50
Kinabatangan	5° 29’ N, 118° 08’ E	260	High. Relatively isolated, highly degraded patches of forest along large river.	Selectively logged, mosaic of forest types, including riparian forest, seasonally flooded forest, swamp forest, limestone forest.	>20
Malua	5° 08’ N, 117° 40’ E	340	Low. Part of ca. 1 million ha Central Sabah Forest complex	Twice-logged (1960s & 2006-2007), lowland dipterocarp. High density of open logging roads and skid trails.	1

Table 2. Details of camera trap sampling regimes and Sunda clouded leopard photographic capture data derived from surveys of eight forest study areas in Sabah, Malaysian Borneo. [a] Camera trap grid area is defined by a 100% Minimum Convex Polygon around all camera stations. [b]We followed two survey protocols, Split-grid: where the entire grid was sequentially surveyed in two halves, and Simultaneously (Sim): where all camera stations were deployed in a single phase. [c]Number of photographic captures of different individuals or images obtained more than 1 hour apart. [d]Values within parentheses represent capture data for male, females and cubs, respectively.

Study area	Camera trap grid					Survey effort and Sunda clouded leopard capture data			
	Area (km^2) [a]	Protocol [b]	No. cam. stations	No. cam. stations on road / trail	Mean elevation and range (m.a.s.l)	Survey dates	No. trap days	No. independent captures [c, d]	No. different animals recorded [d]
Danum Valley	157.0	Split	79	0 / 79	384 (153–804)	24/3/12–6/10/12	5837	88 (82,6,0)	9 (6,3,0)
Tawau	149.0	Sim.	77	0 / 77	706 (209–1195)	21/10/12–30/12/13	17397	239 (219,20,1)	12 (7,5,1)
Crocker	149.7	Sim.	35	3 / 32	1029 (383–1452)	6/10/12–27/2/12	4059	51 (46,5,2)	8 (4,4,2)
Ulu Segama	60.1	Sim.	22	19 / 3	252 (150–408)	24/5/07–18/10/07	2847	83 (70,13,0)	11 (6,5,0)
Tabin	159.0	Split	74	12 / 74	175 (11–431)	18/09/09–22/4/10	6462	41 (36,5,0)	9 (5,4,0)
Kabili Sepilok	49.4	Sim.	35	0 / 35	66 (8–134)	9/2/11–25/5/11	2054	0	0
Kinabatangan	359.5	Split	66	0 / 66	35 (5–135)	24/7/10–17/12/10	4340	15 (8,7,0)	5 (2,3,0)
Malua	102.8	Sim.	38	38 / 0	177 (68–286)	9/7/08–12/2/09	3869	11 (9,2,1)	6 (4,2,1)

Table 3. Sampling specifications and Sunda clouded leopard capture data from the closed survey periods from seven study areas in Sabah, Malaysian Borneo. [a] Number of independent photographic captures that were used in the SECR analysis. [b] Values in parentheses represent values for males, females and cubs, respectively. [c] Values in parentheses represent the number of different camera stations that each individual was recorded at during the closed survey period.

Study area	Closed survey period	No. sampling occasions	No. trap days	No. captures [a,b]	No. different animals recorded [b]	No. captures per individual [c]	
						Males	Females
Danum Valley	23/06/2012 – 20/09/2012	90	3376	46 (43,3,0)	8 (6,2,0)	23(13), 8(5), 7(4), 2(2), 2(1), 1(1)	2(2), 1(1)
Tawau	11/3/2013 – 8/6/2013	90	6471	101 (92,9,0)	10 (5,5,0)	49(24), 30(17), 7(4), 4(3), 2(2)	3(3), 3(2), 1(1), 1(1), 1(1)
Crocker	17/11/2011 – 14/02/2012	90	3005	37 (34,3,2)	6 (3,3,2)	21(11), 9(3), 4(1)	1(1), 1(1), 1(1)
Ulu Segama	21/06/2007 – 18/09/2007	90	1980	59 (48,11,0)	10 (6,4,0)	22(6), 10(6), 6(4), 5(3), 3(1), 2(1)	5(4), 2(2), 2(1), 1(1)
Tabin	11/11/2009 – 10/3/2010	120	3677	21 (18,3,0)	8 (5,3,0)	10(6), 4(4), 2(2), 1(1), 1(1)	1(1), 1(1), 1(1)
Kinabatangan	20/8/2010 – 17/11/2010	90	3060	13 (7,6,0)	5 (2,3,0)	6(3), 1(1)	4(4), 1(1), 1(1)
Malua	30/9/2008 – 28/12/2008	90	2577	10 (8,2,1)	6 (4,2,1)	3(2), 2(2), 2(1), 1(1)	1(1), 1(1)

Table 4. [a]Indication of relative poaching pressure in each study area based on photographic detection rate of presumed poachers and percentage of camera traps stolen; see methods for full description.

Study area	Mean hunter encounter rate ±SD [a]	% camera stolen
Danum Valley	0.000 ±0.000	0
Ulu Segama	0.071 ±0.228	0
Tawau	0.090 ±0.455	1.3
Kabili-Sepilok	0.144 ±0.704	5.7
Crocker	0.288 ±0.642	11.1
Tabin	0.381 ±2.366	2.7
Kinabatangan	0.434 ±1.138	6.1
Malua	0.576 ±0.899	26.3

Table 5. Posterior summaries of the Bayesian-SECR model parameters of camera trap data of the Sunda clouded leopard from six study areas in Sabah, Malaysian Borneo. 95% HPD: the Bayesian highest posterior density interval, that is the shortest interval enclosing 95% of the posterior distribution; σ: movement parameter, related to home range radius; λ_0: baseline trap encounter rate, the number of independent photographic detections per day; ψ: the ratio of the estimated abundance within the state space to the maximum allowable number defined by the augmented value; *N*: number of individuals in the state space; *D*: density ±SD (individuals per 100 km^2).

Parameter	Danum Valley		Tawau Hills		Crocker		Ulu Segama		Tabin		Kinabatangan	
	Mean ±SD	95% HPD	Mean ±SD	95% HPD	Mean ±SD	95% HPD	Mean ±SD	95% HPD	Mean ±SD	95% HPD	Mean ±SD	95% HPD
σ	3074 ±432	2341–3937	3915 ±354	3284–4625	3688 ±479	2815–4638	2692 ±408	1970–3470	4649 ±1616	2325–7575	9104 ±2672	5151–13986
λ_0	0.017 ±0.004	0.009–0.025	0.013 ±0.002	0.009–0.017	0.023 ±0.006	0.012–0.035	0.043 ±0.015	0.020–0.072	0.004 ±0.002	0.001–0.007	0.003 ±0.002	0.001–0.007
ψ	0.353 ±0.118	0.142–0.591	0.400 ±0.111	0.194–0.619	0.283 ±0.100	0.100–0.480	0.319 ±0.118	0.114–0.555	0.284 ±0.122	0.084–0.529	0.316 ±0.146	0.072–0.609
N	25.5 ±8.0	12.0–41.0	19.8 ±4.6	11.0–28.0	12.6 ±3.7	7.0–20.0	44.3 ±15.9	18.0–76.0	30.3 ±12.6	9.0–54.0	26.5 ±12.0	7.0–50.0
D	1.73 ±0.54	0.81–2.78	2.23 ±0.52	1.35–3.27	1.39 ±0.41	0.77–2.21	3.10 ±1.11	1.26–5.32	2.66 ±1.11	0.79–4.74	1.54 ±0.70	0.41–2.90
p-value	0.523		0.573		0.501		0.496		0.697		0.606	

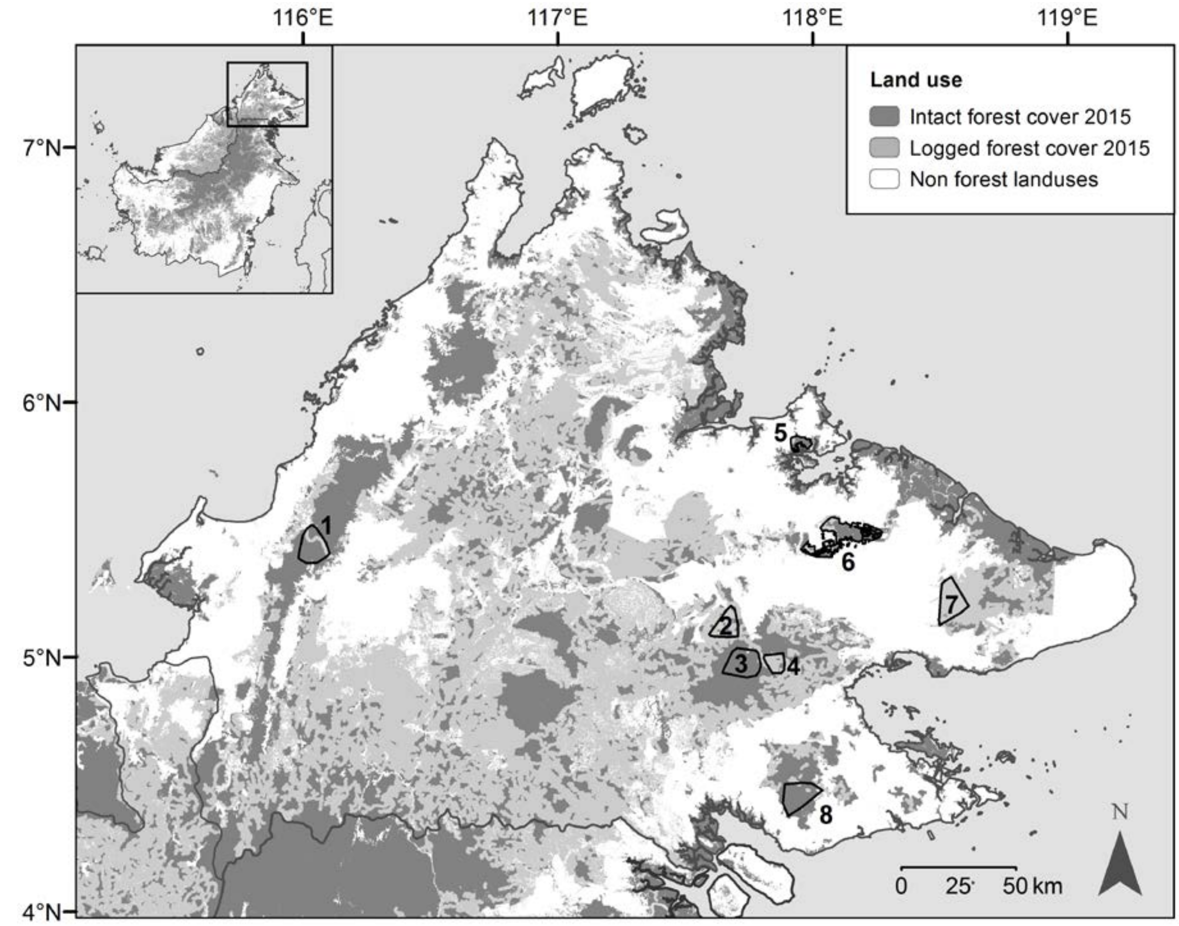

Fig 1. The locations of the eight camera trap survey areas in Sabah, Malaysian Borneo, showing land use in 2015. Numbered polygons represent the different study areas: 1. Crocker Range Park; 2. Malua Forest Reserve; 3. Danum Valley Conservation Area; 4. Ulu Segama Forest Reserve; 5. Kabili-Sepilok Forest Reserve; 6. Lower Kinabatangan Wildlife Sanctuary; 7. Tabin Wildlife Reserve; 8. Tawau Hills Park. Inset shows the island of Borneo. Land use data derived from Gaveau et al. (2016). Note, intact forest includes both primary forest as well as previously logged forest, the impacts of which were no longer visible via analysis of satellite images in 2015; see Gaveau et al. (2016) for further details.