

RESEARCH ARTICLE

Home range variation and site fidelity of Bornean southern gibbons [*Hylobates albibarbis*] from 2010-2018

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Abstract

Gibbons are highly territorial and have two key areas within these territories. The core area in which we find all sleeping trees and the trees from which the gibbons duet and the wider home range (HR) which has varying levels of overlap with neighbouring gibbon groups. The core area is strenuously defended, with the wider HR being more of a shared area for neighbouring groups. We present ranging and movement data on four wild gibbon groups from January 2010 to July 2018. Global Positioning System (GPS) data were collected every 5 mins on habituated groups in Sebangau, Central Kalimantan, Indonesia resulting in 35,521 waypoints. Gibbon home- and corerange sizes were calculated using 95%, and 50%, volume contours of kernel density estimates. Home-ranges ranged from 58.74–147.75 ha with a mean of $95.7 \pm \text{SD } 37.75$ ha, the highest of comparable *Hylobates* species. Core-range size ranged from 20.7–51.31 ha with a mean size of $31.7 \pm \text{SD } 13.76$ ha. Gibbons had consistent site fidelity for their home- and core ranges; percentage overlap ranged from 4.3–23.97% with a mean $16.5 \pm \text{SD } 8.65\%$ overlap in home-range area. Core ranges did not overlap with the exception of two groups, in which a 0.64 ha (2.69%) overlap occurred. Unsurprisingly forest loss from fire does affect the location of the HR of the impacted group, but does not appear to affect adjacent groups, though more data are needed on this. Understanding the complex use of space of these territorial animals is important in assessing both carrying capacity for wild populations and understating how reintroduced gibbon pairs will establish their core and HR.

Introduction

Home range is defined as the area in which an animal normally travels during routine activities, such as food gathering, mating and caring for young [1]. Home range estimation is important for the understanding of the species' spatial and behavioural ecology [2–4]. Information

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about ranging patterns and its' determinants are important for several reasons: this constitutes basic data for the study of social organization of a species, gives an indicator of the spatial needs for individuals and populations, and provides essential tools for conservation management, especially for species found in small, isolated or endangered habitats [2,5,6].

The first descriptions of territorial and space use in gibbons are given [7,8] and [9,10], studying the concept of territoriality, disputes between groups, and home range determinants. Global Positioning Systems (GPS) data allow researchers to analyse animal's spatial use and relate it to behavioural and socio-ecology. It is useful to analyse the determinants which influence home range size and what influences home range sizes between groups in the same habitat [11–14]. Patterns of ranging behaviour can be influenced by the distribution and abundance of food trees [15–19], phenology [20,21], body size [22–24], group size [25–28], location of night trees [29–35], interaction between conspecific groups [36] and the need to patrol territorial boundaries [37–41]. Calculating home range overlap provides information about the area shared between groups, this area represents a shared space where gibbons compete for food resources. Territorial disputes between gibbons take place along the boundary where ranges overlap, and seems that these disputes appear to occur as a result of chance encounters between groups near the boundary [41]. Gibbon territories can be influenced by food availability, canopy cover [18,42,43], presence of tall emergent trees from which to sing [44–46] and suitable sleeping sites [30,33,34,47]. Spacing of gibbons is regulated by both direct encounters [9,41,48,49] and by singing [45] with elements of the song (duet or coda) travelling over varying distances thus carrying information both intra- and inter-group [46].

The study area was impacted by the forest fires in 2015, which caused widespread habitat loss across Borneo and Sumatra [50–53]. For this reason, we also want to understand how loss of forest could impact established home ranges for gibbons.

In this study we present the first long-term assessment on gibbon movement in a peat-swamp forest, specifically focussing on three key analyses:

1. Home range size and changes over time,
2. Home range location, site fidelity and changes over time,
3. Home range overlap between groups and changes over time and
4. Investigating the impact of the 2015 fires on gibbon home ranges.

Materials and methods

The study site is the National Laboratory of Peat Swamp Forest (NLPSF) managed by CIM-TROP (Centre for the International Cooperation in management of Tropical Peatland). NLPSF is located at the NE part of the Sebangau Forest, Central Kalimantan, Indonesia (Fig 1). Sebangau catchment covers an area of 5600 km² of peat-swamp forest [54,55]. The research area is 4 km² of grid transects system, containing seven habituated gibbon groups. The Sebangau catchment is characterised by peat-swamp forest and low elevation, presenting three different forest types: mixed swamp forest, low pole forest and tall interior forest [56]. Our study was carried in Mixed Swamp Forest (MSF) which occupies 40% of the total area of Sebangau forest [57]. The MSF extends ~4km from the margin of the forest into the interior. It is beyond the location of the river flooding zone. The forest is tall and stratified with an upper canopy at ~35m, a closed layer between 15–25m and an understorey of smaller trees at 7–12m. Trees grown on hummocks interspersed with hollows which fill with water during the wet season. Many of the species have stilt or buttress root systems and pneumatophores are common. Typical trees of the upper and mid-canopy are *Aglaia rubinigosa*, *Calophyllum hosei*, *C. lowii*, *C.*

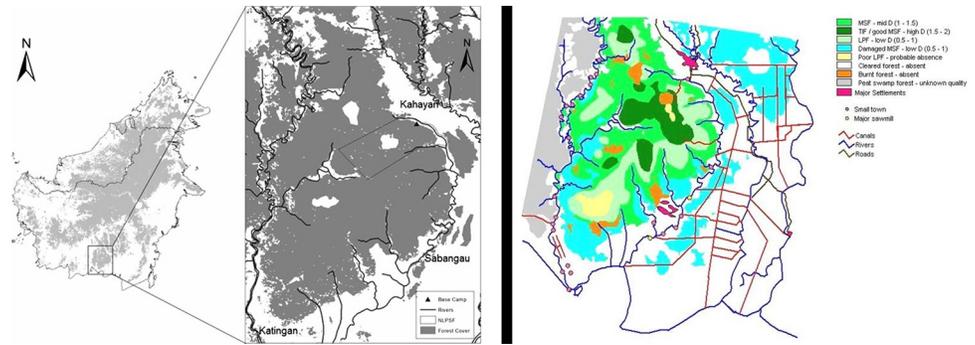


Fig 1. (a) Location of the Natural Laboratory for the Study of Peat-Swamp Forest (NLPSF) within Sabangau tropical peat-swamp forest and Borneo. Forest cover is shaded gray, non-forested areas white. Adapted from [5]. Fig 1b shows habitat breakdown of the landscape.

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sclerophyllum, *Combretocarpus rotundatus*, *Cratoxylum galucum*, *Dactylocladus stenostachys*, *Dipterocarpus corieus*, *Dyera costulata*, *Ganua mottleyana*, *Gonstylua bancanus*, *Mezettia leptopoda* [58], *Neoscortechinia kingii*, *Palaquium cochlearifolium*, *P. leiocarpum*, *Shorea blangeran*, *S. teysmanniana* and *Xylopia fusca* [54,59].

GPS data collection began in May 2005 on seven groups but because of issues with historic satellite accuracy and inconsistent survey effort we present only data from January 2010 to July 2018 on four groups. Group Composition is presented in Table 1. Gibbons were identified using photographs, presence of infants and distinguishing features to create ID sheets for each gibbon in each group including data on HR location and singing trees. ID Book is provided in S1 Table. Only adult gibbons were selected as the focal animal.

Two groups (Group C and Group K) were followed extensively, yielding a nine-year dataset for inter-year comparison of home- and core-range fluctuations; two other groups yielded enough home-range data points to conduct home-range analysis (Table 2). Gibbon groups were located before dawn using their calls as a reference if no sleeping tree location (i.e. the last known location of the group in which they slept from the previous day's follow). Gibbons are followed by two researchers who share data collection with one researcher focussing on the focal gibbon and the second researcher collecting GPS data. Instantaneous focal activity data [60] were collected every 5 minutes on a focal adult chosen via an alternate selection method (i.e., the focal adult chosen to be followed on day x_1 would be chosen again on day x_3 , etc.) and positional data were collected using hand-held Global Positioning System units (Garmin GPS

Table 1. Group composition of the four main groups over the duration of the study. AdF = adult female, AdM—adult male, S = subadult, J = juvenile, I = dependent infant.

	A	C	K	M
2010	AdF, AdM, SM, JF	AdF, AdM, SF, JM	AdF, AdM, SF, JF	AdF, AdM, SF, JM, IM
2011	AdF, AdM, SM, JF	AdF, AdM, SF, JM	AdF, AdM, SF, JF	AdF, AdM, SF, JM, IM
2012	AdF, AdM, SM, JF, IF	AdF, AdM, SF, JM, IM	AdF, AdM, SF, JF, IF	AdF, AdM, SM, JM,
2013	AdF, AdM, SM, JF, IF	AdF, AdM, SF, JM, IM	AdF, AdM, SF, JF, IF	AdF, AdM, SM, JM,
2014	AdF, AdM, SF, JM,	AdF, AdM, SM, JM,	AdF, AdM, SF, JF	AdF, AdM, SM, JM,
2015	AdF, AdM, SF, JM,	AdF, AdM, SM, JM,	AdF, AdM, SF, JF	AdF, AdM, SM, JF, IF
2016	AdF, AdM, SF, JM,	AdF, AdM, SM, JM,	AdF, AdM, SF, IF, IF	AdF, AdM, SM, JF, IF
2017	AdF, AdM, SM, IM	AdF, AdM, SM, JM, IM	AdF, AdM, SF, IF, IF	AdF, AdM, SF, JF
2018	AdF, AdM, SM, IM	AdF, AdM, SM, JM, IM	AdF, AdM, SF, IF, IF	AdF, AdM, SF, JF

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Table 2. Summary data of all four groups including survey effort [years and datapoints].

	# Years data	Average waypoints/year	Total # waypoints
A	3	109	326
C	9	1,946	17,517
K	9	1,901	17,111
M	1	NA	567
	TOTAL		35,521

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12XL, and 60Csx with an accuracy of minimum 5–8 meters at each locality) during daily follows, on the same 5 minute instant, and also at every feeding tree (see [61]). Signal is sufficient to obtain accurate GPS locations at 5-min intervals. If the accuracy was >8m then the point was discarded. Hand-drawn maps are also used on every behavioural follow of gibbons. By splitting the data collection and having 2 researchers we are able to obtain accurate positional and behavioural data on the habituated groups [61]. All GPS locality data were converted into ‘xy’ coordinates using DNR GPS Application (University of Minnesota 2012). Estimates of home-range sizes were obtained using the kernel density estimate method [62] using the ‘ade-HabitatHR’ package [63] in the statistical software package ‘R’ [64]. A volume contour of 95% of kernels analysed was considered the home range a volume contour of 50% of kernels analysed was considered the core range. The home-range analysis used the ‘href’ bandwidth for kernel smoothing. For further details see [63].

Results

HR overlap

Overlap ranged from 3.52% to 23.97% of the total home range (Table 3). Home Range values for each group for each study year and change in size of HR are available in S2 Table (all in Km²).

Home range size and changes over time

Home-range and core-range sizes for Group C and Group K were relatively stable over time (Figs 2 and 3): Group C Core 18.89ha (range 7.68–23.58ha) HR 55.84ha (range 28.66–74.74ha) and Group K Core 50.07ha (range 27.24–68.79ha) HR 153.96ha (range 120.75–237.73ha).

The variation in GPS localities year on year is unlikely to cause error in home-range estimation. Core-ranges localities were fairly constant (Fig 4).

Gibbons had consistent site fidelity for their home- and core ranges; percentage overlap ranged from 4.3 to 23.97% with a mean 16.5 ± SD 8.65% overlap in home-range area (Fig 5).

Core ranges did overlap: Group K and C, in which a 0.14ha overlap (equal to 23.72% of Group C HR and 9.45% of Group K HR) occurred and Group K and M where there was a 0.2ha overlap (equal to 13.51% of Group K HR and 21.05% of Group M HR). The total forest area covered by each group remains stable over the course of the study, as does overlap (Fig 6).

Table 3. Overlap between study groups.

	C	K	M
A	3.52 ha (4.3%)	13.69 ha (16.8.3%)	
C		14.08 ha (23.97%)	
K			19.82 ha (20.93%)
M			

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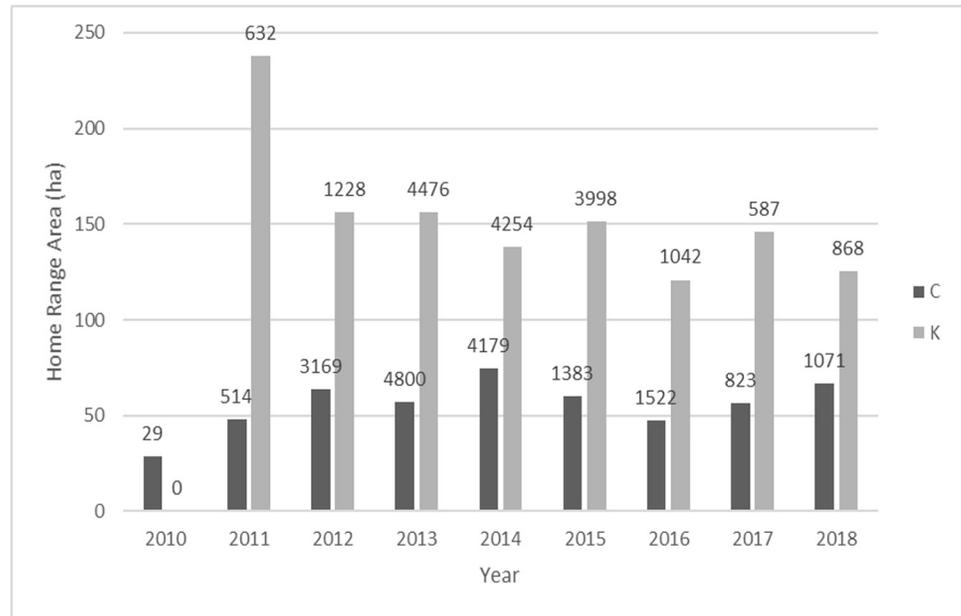


Fig 2. Average 95% HR size for all years and number of GPS points.

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HR and fire

In the fires in 2015 there was a loss of 10% of the forest (53.8km², BNF unpublished data). For the groups for which there are data pre-and post 2015 fires was virtually no change in the HR location of Groups C or K following forest loss in the 2015 fires, but there was a change in HR of Group A as the fires directly affected the HR of Group A (Fig 7). Group A appear to have moved west away from the burnt area.

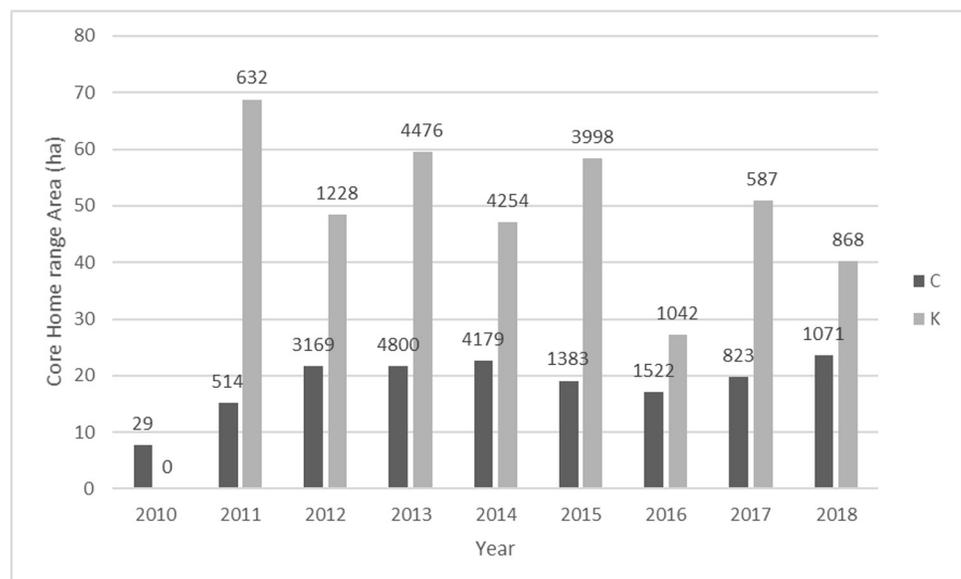


Fig 3. Average 95% core size for all years and number of GPS points.

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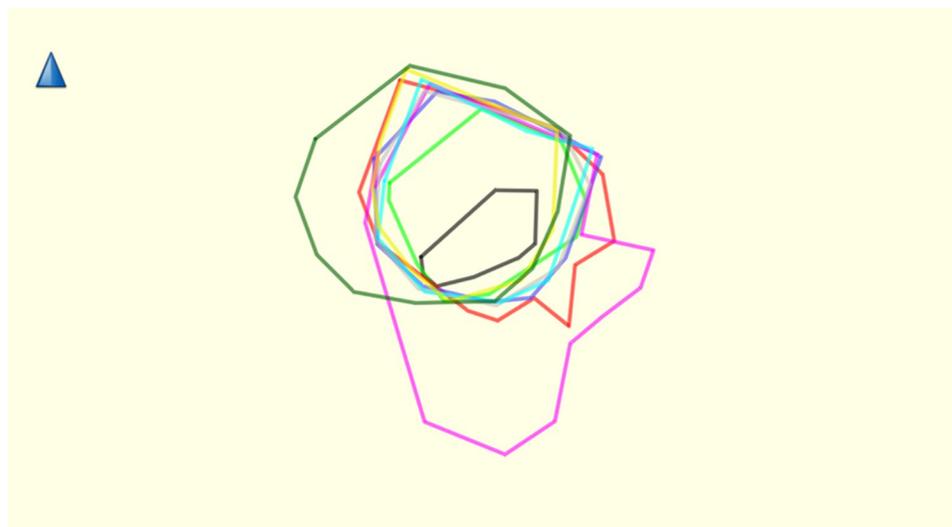


Fig 4. Showing site fidelity of Group C. 2010 = black, 2011 = light green, 2012 = red, 2013 = blue, 2014 = pink, 2015 = light grey, 2016 = light blue, 2017 = yellow and 2018 = dark green. Created using Garmin BaseCamp V 4.7.0.

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Discussion

The HR of the gibbons from Sebangau are the largest of all comparable *Hylobates* sp. studies (Table 4). A possible explanation is the peat-swamp habitat and associated variable food availability [18,56,65–68] and/or the population density of the area being lower than carrying capacity due to anthropogenic disturbances e.g. logging and fire [43,69–71].

Core areas were where the gibbons slept and sang their morning duets. These areas were vigorously defended and do not overlap [61,83] whereas the home range area did overlap with other groups and feeding trees were shared between groups [trees are tagged with unique numbers]. Thus feeding takes place across both the core and HR of the territory, singing and

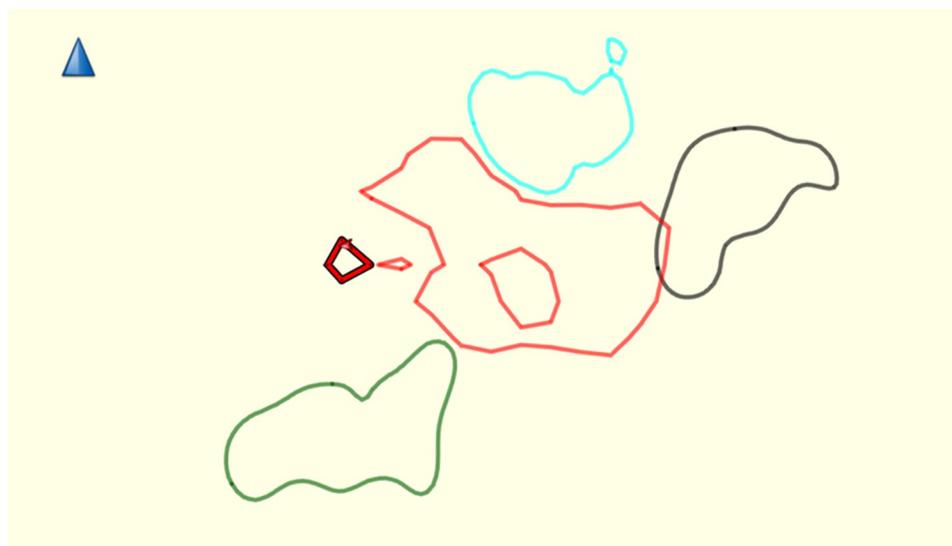


Fig 5. Average 50% core HR size for all years and number of GPS points. Group A = Black; Group C = Light Blue; Group K = Red; Group M = Green. Created using Garmin BaseCamp V 4.7.0.

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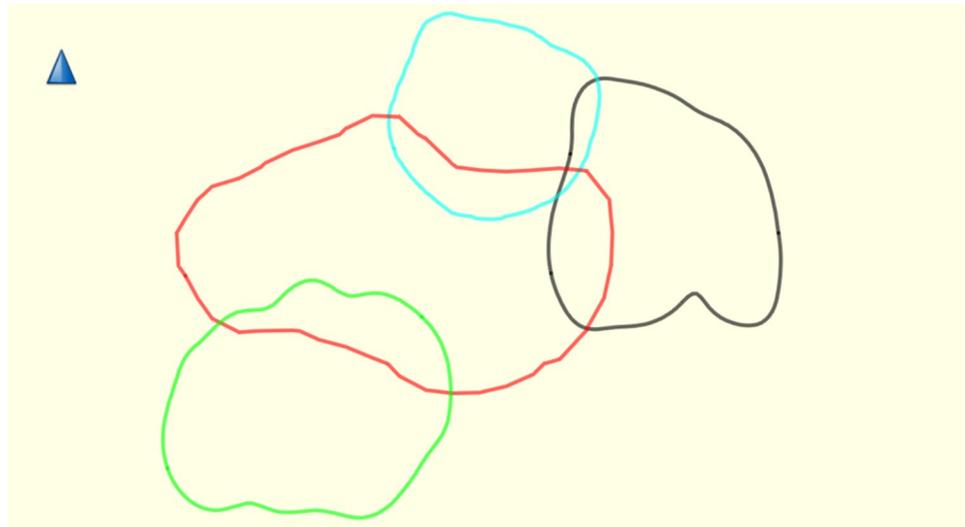


Fig 6. Average 95% HR size for all years and number of GPS points. Group A = black, Group C = light blue, Group K = red and Group M = green. Created using Garmin BaseCamp V 4.7.0.

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sleeping only in the core and all is defended. None of the intergroup encounters occur in the core of any of the four groups [18,30,46].

We demonstrate that gibbons have significant site fidelity for their home ranges, they do have consistent overlap with neighbouring groups [61,77] and there is some annual movement for all groups in the position of the centrepoint of their HR. Unsurprisingly forest loss from fire does affect the location of the HR of the impacted group, but does not appear to affect adjacent groups, though more data are needed on this. Given how fixed HR's are for gibbons, loss of forest will affect the size of the HR, the ability for the group to access food and ultimately could result in groups being compressed into a small area of suitable forest surrounded by unsuitable forest, creating over-crowding and limited dispersal options for sub-adults [84]. Hence why the average HR overlap of 18.76% is much smaller than that reported from other studies: 65% [77] and 79% [75].

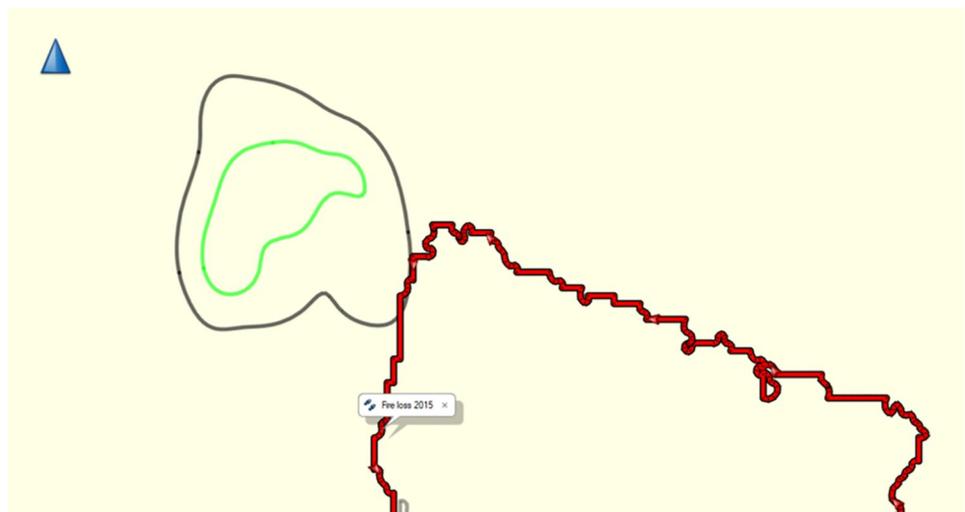


Fig 7. Forest loss to fire (red area) and HR of Group A (50% green, 95% black). Created using Garmin BaseCamp V 4.7.0.

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Table 4. Comparison of gibbon Hr sizes across species. Studies were selected which use similar methods for HR estimation.

Species	Country	Site and # groups included	Average HR km ²	Reference
<i>Hoolock hoolock</i>	India	Garo Hills (7)	0.003	[72]
<i>Hylobates lar</i>	Indonesia	Khao Yai (11)	0.180	[73]
<i>Hylobates lar</i>	Thailand	Khao Yai (2)	0.230	[74]
<i>Hylobates agilis</i>	Indonesia	Limau Manis (2)	0.240	[75]
<i>Hylobates albibarbis</i>	Indonesia	Gunung Palung (3)	0.280	[76]
<i>Hylobates lar</i>	Thailand	Khao Yai (7)]	0.280	[77]
<i>Hylobates moloch</i>	Indonesia	Gunung Halimun-Salak National Park (3)]	0.370	[78]
<i>Hylobates albibarbis</i>	Indonesia	Sebangau (7)	0.96	This study
<i>Nomascus nasutus</i>	China	Cao Vit Gibbon Conservation Area [Vietnam] and Bangliang Gibbon Nature Reserve China (6)	1.300	[79]
<i>Nomascus concolor</i>	China	Mt. Wuliang (1)	1.500	[80]
<i>Nomascus hainanus</i>	China	Hainan (3)	4.850	[81]
<i>Nomascus leucogenys</i>	China	Yunnan (2)	5.400	[82]

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The fires did not impact the territories of Groups C, K or M due to fires being brought under control by teams of fire-fighters. Despite this effort, some of the forest did burn in the area of Group A's territory, thus pushing the group further west. There are major negative impacts of Borneo peat/forest fire on biodiversity, affecting large numbers of species from Kalimantan-wide to site scale. Known/suspected impacts include respiratory ailments in animals, e.g. orangutans [Borneo Orangutan Survival Foundation, pers. comm.]; reduced gibbon territorial singing [85] and orangutan calling [86] and changes in phenology [87,88]. These and other as yet unknown impacts are expected to continue and worsen unless the underlying causes can be tackled, adding an additional major threat to biodiversity and increasing extinction risk for many species. Understanding the complex use of space of these territorial animals is important in assessing both carrying capacity [43,89], how dispersing gibbons use space and establish a territory [9,90–92] and understanding how reintroduced gibbon pairs will establish their core and HR [93–97].

Hunting, fire, forest clearance and forest fragmentation are all impacting Borneo's gibbons. Gibbons need large areas to survive and linking forests and reducing fragmentation is the key to their conservation. Landscapes and connectivity depend on collaboration between local and international governments, communities, conservation organizations and researchers. As we understand more about gibbon habitat use we will begin to see how best to connect the remaining forest.

Supporting information

S1 Table. Identification tables for Group C as an example of how gibbons are distinguished from each other.

(DOCX)

S2 Table. Home Range values for each group for each study year and change in size of HR (all in Km²).

(DOCX)

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BRC: 35/EXT/SIP/FRP/SM/VII/2015. DES: 255/SIP/FRP/SM/VII/2012.

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References

1. Jolly A. The evolution of primate behaviour. Macmillan. NY: MacMillan Co.; 1972.
2. Mitani JC, Rodman PS. Territoriality: The relation of ranging pattern and home range size to defensibility, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol.* 1979; 5:241–51.
3. Digby LJ. A new approach to primate home ranges: using 3D and 4D data to calculate home range “volume” and use. Lee PC, Honess P, Buchanan-Smith H, MacLarnon A, Sellers WI, editors. XXII Congress of the International Primatological Society. Edinburgh: Top Copy, Bristol, UK; 2008.
4. Ehlers Smith DA, Ehlers Smith YC, Cheyne SM. Home-Range Use and Activity Patterns of the Red Langur (*Presbytis rubicunda*) in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesian Borneo. *Int J Primatol.* 2013; 34(5).
5. Hemingway CA, Bynum N. The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP, editors. *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates.* Cambridge: Cambridge University Press; 2005. p. 57–104.
6. Vogel ER, Haag L, Mitra-Setia T, van Schaik CP, Dominy NJ. Foraging and ranging behavior during a fallback episode: *Hylobates albobarbis* and *Pongo pygmaeus wurmbii* compared. *Am J Phys Anthropol.* 2009; 140:716–26.
7. Carpenter CR. A field study in Siam of the behaviour and social relations of the gibbon *Hylobates lar*. *Comp Psychol Monogr.* 1940; 16(1–212).
8. Carpenter CR. Behaviour and social relations of free-ranging primates. *Sci Mon.* 1939; 43:319–25.

9. Ellefson JO. Territorial behaviour in the common white-handed gibbon, *Hylobates lar*. In: Jay PC, editor. *Primates: studies in adaptation and variability*. NY: Holt; 1968. p. 180–99.
10. Ellefson JO. A natural history of white handed gibbons in the Malayan peninsula. *Gibbon and Siamang*. 1974; 3: 1–136.
11. Ehlers Smith DA, Ehlers Smith YC, Cheyne SM. Home Range Use and Activity Patterns of Red Langurs in Sabangau Tropical Peat-Swamp Forest, Central Kalimantan, Indonesia. *Int J Primatol*. 2013; 34(5):957–72.
12. Singleton I, van Schaik CP. Orangutan home range size and its determinants in a Sumatran swamp forest. *Int J Primatol*. 2001; 22(6):877–911.
13. Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L. Dispersed Male Networks in Western Gorillas. *Curr Biol*. 2004; 14:153–510.
14. Link A, DiFiore A. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *J Trop Ecol*. 2006; 22:235–46.
15. Bennet EL. Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos*. *Folia Primatol*. 1986; 47:26–38. <https://doi.org/10.1159/000156261> PMID: 3557228
16. Ma C, Fan PF, Zhang ZY, Li JH, Shi XC, Xiao W. Diet and feeding behavior of a group of 42 Phayre's langurs in a seasonal habitat in Mt. Gaoligong, Yunnan, China. *Am J Primatol*. 2017; 79(10).
17. Lewis MC, O'Riain MJ. Foraging Profile, Activity Budget and Spatial Ecology of Exclusively Natural-Foraging Chacma Baboons (*Papio ursinus*) on the Cape Peninsula, South Africa. *Int J Primatol*. 2017; 38(4).
18. Singh M, Cheyne SM, Ehlers Smith DA. How conspecific primates use their habitats: Surviving in an anthropogenically-disturbed forest in Central Kalimantan, Indonesia. *Ecol Indic*. 2018; 87:167–77.
19. Rodman PS. Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: Clutton-Brook TH, editor. *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London, UK: Academic Press, London, 381–413.; 1977. p. 171–209.
20. van Schaik CP, Terborgh JW, Wright SJ, Terbourgh JW, Joseph Wright S. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Ann Rev Ecol Syst*. 1993; 24:353–77.
21. Marshall AJ, Ancrenaz M, Brearley FQ, Fredriksson GM, Ghaffar N, Heydon M, et al. The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans. In: Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP, editors. *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*. Oxford: Oxford University Press; 2009. p. 97–116.
22. Terborgh J. *Five new world primates: A study in comparative ecology*. Princeton: Princeton University Press; 1983.
23. Mitani JC. Orangutan activity budgets: Monthly variations and the effects of body size, parturition, and sociality. *Amer J Primatol*. 1989; 18(2):87–100.
24. Olupot W. Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conserv Biol*. 2000; 14(3):833–43.
25. Wrangham RW, Gittleman JL, Chapman CA. Constraints in group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol*. 1993; (32):199–209.
26. Overdorff DJ. Ecological correlates to social structure in two Lemur species in Madagascar. *Am J Phys Anthropol*. 1996; 100(4):487–506. [https://doi.org/10.1002/\(SICI\)1096-8644\(199608\)100:4<487::AID-AJPA4>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1096-8644(199608)100:4<487::AID-AJPA4>3.0.CO;2-O) PMID: 8842323
27. Hashimoto C, Tashiro Y, Kimura D, Enomoto T, Ingmanson EJ, Idani G, et al. Habitat use and ranging of wild bonobos (*Pan paniscus*) at Wamba. *Int J Primatol*. 1998; 19(6):1045–60.
28. Carretero-Pinzón X, Defler TR, McAlpine CA, Rhodes JR. What do we know about the effect of patch size on primate species across life history traits? *Biodivers Conserv*. 2016; 25(1).
29. Cheyne SM, Rowland D, Höing A, Sheeran LK. How orang-utans choose where to sleep: comparison of nest site variables. *Asian Primates J*. 2013; 3(1):13–7.
30. Cheyne SMM, Höing A, Rinear J, Sheeran LKK. Sleeping site selection by agile gibbons: The influence of tree stability, fruit availability, and predation risk. *Folia Primatol*. 2013; 89(3–6):299–311.
31. Svensson MS, Nekaris KAI, Bearder SK, Bettridge CM, Butynski TM, Cheyne SM, et al. Sleep patterns, daytime predation, and the evolution of diurnal sleep site selection in loriforms. *Am J Phys Anthropol* [Internet]. 2018; 166(3):563–77. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1002/ajpa.23450> PMID: 29989160
32. Hamilton WJ III. Baboon sleeping site preferences and relationships to primate grouping patterns. *Am J Primatol*. 1982; 3:41–53.

33. Chetry D, Chetry R, Ghosh K. Sleeping Tree Selection by Sympatric Primates in Gibbon Wildlife Sanctuary, Assam, India. In: International Primatological Society. Edinburgh; 2008. p. 403.
34. Fei H, Scott MB, Zhang W, Ma C, Xiang Z, Fan P. Sleeping tree selection of Cao Vit gibbon (*Nomascus nasutus*) living in degraded karst forest in Bangliang, Jiangxi, China. *Am J Primatol* [Internet]. 2012; 74. Available from: <https://doi.org/10.1002/ajp.22049>
35. Fan P-F, Jiang X-L. Sleeping sites, sleeping trees, and sleep-related behaviors of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China. *Am J Primatol*. 2008; 70:153–60. <https://doi.org/10.1002/ajp.20470> PMID: 17854056
36. Sekulic R. Daily and seasonal patterns of roaring and spacing in four howler *Alevatta enniculus* troops. *Folia Primatol*. 1982; 39:22–48. <https://doi.org/10.1159/000156067> PMID: 6890502
37. Whitten AJ. Home range use by Kloss gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Anim Behav*. 1982; 30:182–98.
38. MacKinnon J, MacKinnon K. Territory, monogamy and song in gibbons and tarsiers. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh: Edinburgh University Press; 1984. p. 291–7.
39. Tenaza RR. Territory and monogamy among Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Primates*. 1975; 24:60–80.
40. Gittins SP. Territorial advertisement and defense in gibbons. In: Preuschoft HH, Chivers DJ, Brockelman WY, Creel N, editors. *The Lesser Apes: Evolutionary and Behavioural Biology*. Edinburgh University Press; 1984. p. 420–4.
41. Gittins SP. Territorial behaviour in the agile gibbon. *Int J Primatol*. 1980; 1(4):381–99.
42. Hamard MCL, Cheyne SMM, Nijman V. Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. *Am J Primatol* [Internet]. 2010; 72(7):607–16. Available from: <http://dx.doi.org/10.1002/ajp.20815> PMID: 20186760
43. Cheyne SM, Gilhooly LJ, Hamard MC, Höing A, Houlihan PR, Kursani, et al. Population mapping of gibbons in Kalimantan, Indonesia: Correlates of gibbon density and vegetation across the species' range. *Endanger Species Res*. 2016; 30(1):133–43.
44. Geissmann T, Nijman V. Calling in wild silvery gibbons (*Hylobates moloch*) in Java (Indonesia): Behavior, phylogeny, and conservation. *Am J Primatol*. 2006; 68(1):1–19. <https://doi.org/10.1002/ajp.20203> PMID: 16419119
45. Mitani JC. Gibbon song duets and interspacing behaviour. *Behaviour*. 1985; 92:59–96.
46. O'Hagan R., Ward L, Cheyne SM. Gibbon (*Hylobates albibarbis*) Duet Song Propagation Distance: Implications for Intra- and Inter-Group Communication. *J Acoust Acoust*. 2019; in review.
47. Inoue Y, Sinun W, Okanoya K. Activity budget, travel distance, sleeping time, height of activity and travel order of wild East Bornean Grey gibbons (*Hylobates funereus*) in Danum Valley Conservation Area. *Raffles Bull Zool*. 2016; 64.
48. Leighton D. *Monogamy and Territoriality in Muellers Gibbon*. University of California, Davis; 1984.
49. Palombit RA. Lethal territorial aggression in a white-handed gibbon. *Am J Primatol*. 1993; 31:311–8.
50. Miettinen J, Shi C, Liew S. Fire Distribution in Peninsular Malaysia, Sumatra and Borneo in 2015 with Special Emphasis on Peatland Fires. *Environ Manage*. 2017; 60(4):747–757. <https://doi.org/10.1007/s00267-017-0911-7> PMID: 28674917
51. Siegert F, Ruecker G, Hinrichs A, Hoffmann AA. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature*. 2001; 414:437–40. <https://doi.org/10.1038/35106547> PMID: 11719802
52. Limin S, Jaya A, Siegert F, Rieley JO, Page SE, Boehm HD V. Tropical peat and forest fire in 2002 in Central Kalimantan, its characteristics and the amount of carbon released. In: Päivänen J, editor. *Wise Use of Peatlands (Vol I) Proceedings of the 12th International Peat Congress, Tampere, Finland, 6–11 June 2004*. Saarijärvi, Finland: Saarijärven Offset Oy; 2004. p. 679–86.
53. Wich SA, Singleton I, Nowak MG, Utami Atmoko SSuci, Nisam G, Arif SMhd, et al. Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Sci Adv*. 2016; 2(3).
54. Page SE, Rieley JO, Shotyk ØW, Weiss D. Interdependence of peat and vegetation in a tropical peat swamp forest. *Philos Trans R Soc London B*. 1999; 354:1807–85.
55. Page SE. The biodiversity of peat swamp forest habitats in S.E. Asia; impacts of land-use and environmental change; implications for sustainable ecosystem management. [Internet]. STRAPEAT Project; 2002. <http://www.strapeat.alterra.nl>
56. Cheyne SM, Thompson CJH, Phillips AC, Hill RMC, Limin SH. Density and Population Estimate of Gibbons (*Hylobates albibarbis*) in the Sabangau Catchment, Central Kalimantan, Indonesia. *Primates*. 2008; 49(1):50–6. <https://doi.org/10.1007/s10329-007-0063-0> PMID: 17899314

57. Shepherd PA, Rieley JO, Page SE. The relationship between forest structure and peat characteristics in the upper catchment of the Sungai Sebangau, Central Kalimantan. In: Rieley JO, Page SE, editors. Biodiversity and Sustainability of Tropical Peatlands. Cardigan, UK.: Samara Publishing; 1997. p. 191–210.
58. Lucas PW, Gaskins JT, Lowrey TK, Harrison ME, Morrogh-Bernard HC, Cheyne SM, et al. Evolutionary optimization of material properties of a tropical seed. *J R Soc Interface*. 2011; 9(66):34–42. <https://doi.org/10.1098/rsif.2011.0188> PMID: 21613287
59. Coiner-Collier S, Scott RS, Chalk-Wilayto J, Cheyne SM, Constantino P, Dominy NJ, et al. Primate dietary ecology in the context of food mechanical properties. *J Hum Evol* [Internet]. 2016 Sep 1 [cited 2018 Mar 19]; 98:103–118. Available from: <https://www.sciencedirect.com/science/article/pii/S0047248416300859> PMID: 27542555
60. Altmann J. Observational study of behaviour: sampling methods. *Behaviour*. 1974; 49:227–65. PMID: 4597405
61. Cheyne SM. Behavioural ecology and socio-biology of gibbons (*Hylobates albibarbis*) in a degraded peat-swamp forest. In: Supriatna J, Gursky SL, editors. Indonesian Primates. New York: Springer; 2010. p. 121–56.
62. Worton BJ. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology* [Internet]. 1989; 70(1):164–8. Available from: <https://doi.org/10.2307/1938423>
63. Calenge C. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol Modell* [Internet]. 2006; 197(3):516–9. Available from: <http://www.sciencedirect.com/science/article/pii/S0304380006001414>
64. R Core Team. R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2013. <http://www.r-project.org/>
65. Hamard M, Cheyne SM, Nijman V. Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau Catchment, Central Kalimantan, Indonesia. *Am J Primatol*. 2010; 72(7).
66. Harrison ME, Morrogh-Bernard HC, Chivers DJ. Orangutan Energetics and the Influence of Fruit Availability in the Nonmasting Peat-swamp Forest of Sabangau, Indonesian Borneo. *Int J Primatol*. 2010; 31(4):585–607.
67. Ehlers-Smith DA, Husson SJ, Ehlers Smith YC, Harrison ME. Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: extreme granivory in a non-masting forest. *Am J Primatol*. 2013; 75(8):848–59. <https://doi.org/10.1002/ajp.22148> PMID: 23553789
68. Harrison ME, Zweifel N, Husson SJ, Cheyne SM, D’Arcy LJ, Harsanto FA, et al. Disparity in Onset Timing and Frequency of Flowering and Fruiting Events in Two Bornean Peat-Swamp Forests. *Biotropica*. 2016; 48(2).
69. Harrison M., Hendri, Dragiewicz M., Krisno J, Cheyne SM, Husson SJ. Biodiversity of the Mungku Baru Ulin Forest, Central Kalimantan, Indonesia. Report produced by the Orangutan Tropical Peatland Project for International Animal Rescue. Palangka Raya, Indonesia.: Orangutan Tropical Peatland Project; 2010.
70. Harrison ME, Cheyne SM, Husson SJ, Jeffers KA, Smallcombe J V, Ehlers Smith DA. Preliminary Assessment of the Biodiversity and Conservation Value of the Bawan Forest, Central Kalimantan, Indonesia. Orangutan Tropical Peatland Project Report. Palangka Raya: Orangutan Tropical Peatland Project; 2012.
71. Decker BS. Effects of Habitat Disturbance on the Behavioural Ecology and Demographics of the Tana River Red Colobus (*Colobus badisu rufomitratu*). *Int J Primatol*. 1994; 15(5):703–37.
72. Vasudev D, Fletcher RJ Jr. Incorporating movement behavior into conservation prioritization in fragmented landscapes: An example of western hoolock gibbons in Garo Hills, India. *Biol Conserv*. 2015; 181:124–32.
73. Asensio N, Brockelman WY, Reichard UH, Malaivijitnond S. Gibbon travel paths are goal oriented. *Anim Cogn*. 2010;
74. Bartlett TQ. The Gibbons of Khao Yai: Seasonal Variation in Behavior and Ecology. Pearson, Upper Saddle River; 2009.
75. Koda H, Oyakawa C, Nurulkamilah S, Rizaldi, Sugiura H, Bakar A, et al. Male replacement and stability of territorial boundary in a group of agile gibbons (*Hylobates agilis agilis*) in West Sumatra, Indonesia. *Primates*. 2012; 53(4):327–332. <https://doi.org/10.1007/s10329-012-0313-7> PMID: 22752844
76. Marshall AJ, Cannon CH, Leighton M. Competition and Niche Overlap Between Gibbons (*Hylobates albibarbis*) and Other Frugivorous Vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Lappan S, Whittaker DJ, editors. The Gibbons. Springer Science; 2009. p. 161–88.
77. Savini T, Boesch C, Reichard UH. Home-range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *Am J Phys Anthropol*. 2008; 135(1):1–12. <https://doi.org/10.1002/ajpa.20578> PMID: 17960726

78. Kim S, Lappan S, Choe JC. Diet and Ranging Behavior of the Endangered Javan Gibbon (*Hylobates moloch*) in a Submontane Tropical Rainforest. *Am J Primatol*. 2010; 71:1–11.
79. Fan PF, Jiang XL. Maintenance of Multifemale Social Organization in a Group of *Nomascus concolor* at Wuliang Mountain, Yunnan, China. *Int J Primatol*. 2010; 31(1):1–13.
80. Fan P-F, Jiang X-L. Effects of food and topography on ranging behavior of black crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountain, Yunnan, China. *Am J Primatol*. 2008; 70:871–8. <https://doi.org/10.1002/ajp.20577> PMID: 18548511
81. Bryant JV, Olson VA, Chatterjee HJ, Turvey ST. Identifying environmental versus phylogenetic correlates of behavioural ecology in gibbons: implications for conservation management of the world's rarest ape. *BMC Evol Biol* [Internet]. 2015 Aug; 15(1):171. Available from: <https://doi.org/10.1186/s12862-015-0430-1>
82. Hu Y, Xu HW, Yang DH. Feeding ecology of the white-cheek gibbon (*Hylobates concolor leucogenys*). *Acta Ecol. Sin.* 10 (2), 155–159. *Acta Ecol Sin.* 1990;10(2):155–9.
83. Cheyne SM, Monks EM, Kuswanto Y. An observation of lethal aggression in Bornean agile gibbons *Hylobates albibarbis*. *Gibbon J*. 2010; 6.
84. Cheyne SM, Gilhooly LJ, Hamard MC, Höing A, Houlihan PR, Kursani, et al. Population mapping of gibbons in Kalimantan, Indonesia: Correlates of gibbon density and vegetation across the species' range. *Endanger Species Res*. 2016; 30(1):133–43.
85. Cheyne SM. Effects of Meteorology, Astronomical Variables, Location and Human Disturbance on the Singing Apes: *Hylobates albibarbis*. *Am J Primatol*. 2007; 40(4):1–7.
86. Erb WM, Barrow EJ, Hofner AN, Utami-Atmoko SS, Vogel ER. Wildfire smoke impacts activity and energetics of wild Bornean orangutans. *Sci Rep* [Internet]. 2018; 8(1):7606. Available from: <https://doi.org/10.1038/s41598-018-25847-1> PMID: 29765067
87. Harrison ME, Husson SJ, D'Arcy LJ, Morrogh-Bernard HC, Cheyne SM, van Noordwijk MA, et al. The Fruiting Phenology of Peat-swamp Forest Tree Species at Sabangau and Tuanan, Central Kalimantan, Indonesia. Palangka Raya: The Kalimantan Forests and Climate Partnership; 2010.
88. Harrison ME, Cheyne SM, Sulistiyanto Y, Rieley JO. Biological Effects Of Smoke From Dry-Season Fires In Non-Burnt Areas Of The Sabangau Peat-Swamp Forest, Central Kalimantan, Indonesia. In: The International Symposium and Workshop on Tropical Peatland "Carbon-Climate-Human Interactions—Carbon Pools, Fire, Mitigation, Restoration and Wise Use." Yogyakarta, Indonesia; 2007.
89. Smith JH, King T, Campbell C, Cheyne SM, Nijman V. Modelling Population Viability of Three Independent Javan Gibbon (*Hylobates moloch*) Populations on Java, Indonesia. *Folia Primatol*. 2018; 88(6).
90. Wrangham R, Crofoot M, Lundy R, Gilby I. Use of overlap zones among group-living primates: a test of the risk hypothesis. *Behaviour*. 2007; 144:1599–619.
91. Fischer JO, Geissmann T. Group harmony in gibbons: comparison between the white-handed gibbon (*H. lar*) and siamang (*H. syndactylus*). *Primates*. 1990; 31(4):481–94.
92. Chivers DJ. Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour*. 1976; 57(1–2):116–35.
93. Cheyne SM. Challenges and Opportunities of Primate Rehabilitation—Gibbons as a Case Study. In: Nekaris KAI, Nijman V, Bruford M, Fa J, Godley B, editors. *Endangered Species Research*. Endangered Species Research; 2009. p. 159–65.
94. Cheyne SM. The Role of Reintroduction in Gibbon Conservation: Opportunities and Challenges. In: Lappan SM, Whittaker DL, Geissmann T, editors. *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*. New York: Springer; 2009. p. 477–96.
95. Cheyne SM, Campbell CO, Payne KL. Proposed guidelines for in situ gibbon rescue, rehabilitation and reintroduction. *Int Zoo Yearb*. 2012; 46(1).
96. Campbell CO, Cheyne SM, Rawson B. *Best Practice Guidelines for the Rehabilitation and Translocation of Gibbons*. Gland, Switzerland; 2015.
97. Cheyne SM, Chivers DJ, Sugardjito J. Biology and Behaviour of Released Gibbons. *Biodivers Conserv*. 2008; 17:1741–51.