



**Spatiotemporal requirements of the Hainan gibbon: does home range constrain recovery of the world's rarest ape?**

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1 **Spatiotemporal requirements of the Hainan gibbon: does home range**  
2 **constrain recovery of the world's rarest ape?**

3

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18 Short title: Home range requirements of Hainan gibbon

19 **ABSTRACT**

20 Conservation management requires an evidence-based approach, as uninformed  
21 decisions can signify the difference between species recovery and loss. The Hainan  
22 gibbon, the world's rarest ape, reportedly exploits the largest home range of any  
23 gibbon species, with these apparently large spatial requirements potentially limiting  
24 population recovery. However, previous home range assessments rarely reported  
25 survey methods, effort or analytical approaches, hindering critical evaluation of  
26 estimate reliability. For extremely rare species where data collection is challenging, it  
27 also is unclear what impact such limitations have on estimating home range  
28 requirements. We re-evaluated Hainan gibbon spatial ecology using 75 hours of  
29 observations from 35 contact days over 93 field-days across wet (June 2011-  
30 September 2011) and dry (November 2010-February 2011) seasons. We calculated  
31 home range area for three social groups (N=21 individuals) across the sampling  
32 period, seasonal estimates for one group (based on 24 days of observation; 12 days  
33 per season), and between-group home range overlap using multiple approaches  
34 (Minimum Convex Polygon, Kernel Density Estimation, Local Convex Hull,  
35 Brownian Bridge Movement Model), and assessed estimate reliability and  
36 representativeness using three approaches (Incremental Area Analysis, spatial  
37 concordance, and exclusion of expected holes). We estimated a yearly home range of  
38 1–2 km<sup>2</sup>, with 1.49 km<sup>2</sup> closest to the median of all estimates. Although Hainan  
39 gibbon spatial requirements are relatively large for gibbons, our new estimates are  
40 smaller than previous estimates used to explain the species' limited recovery,  
41 suggesting that habitat availability may be less important in limiting population  
42 growth. We argue that other ecological, genetic, and/or anthropogenic factors are

43 more likely to constrain Hainan gibbon recovery, and conservation attention should  
44 focus on elucidating and managing these factors.

45

46 **Key words:** home range estimation, *Nomascus hainanus*, KDE, LoCoH, spatial  
47 ecology

48

#### 49 **RESEARCH HIGHLIGHTS**

- 50 • Re-evaluation reveals Hainan gibbon home range as c. 1–2 km<sup>2</sup>.
- 51 • Hainan gibbon home range is therefore similar to other *Nomascus* gibbons.
- 52 • Limited data for extremely rare species does not necessarily prevent derivation  
53 of robust home range estimates.

54

55

56 **INTRODUCTION**

57 Effective conservation of all primate species must be grounded in an evidence-based  
58 approach whereby objective, empirical data on threatened species' ecology,  
59 population dynamics and knowledge of current drivers of population decline are used  
60 to guide management decisions [Sutherland et al., 2004; Segan et al., 2011]. For  
61 species of extreme rarity, which persist in small, remnant populations with highly  
62 restricted distributions, accurate decision-making can mean the difference between  
63 extinction and recovery [Groombridge et al., 2004], and generating scientific  
64 baselines on key environmental and population parameters including ranging/space  
65 requirements, social structure, genetic diversity and population status/viability  
66 constitutes an urgent conservation activity [Turvey et al., 2015].

67 The Critically Endangered Hainan gibbon (*Nomascus hainanus*) is the world's rarest  
68 primate, and arguably rarest mammal [Baillie and Butcher, 2012; Schwitzer et al.,  
69 2014]. Following a precipitous twentieth-century decline caused by habitat loss and  
70 hunting [Liu et al., 1984; Zhou et al., 2005], the species now comprises a single  
71 population of approximately 25 individuals, made up of three breeding groups and a  
72 small number of solitary individuals, restricted to a small area of fragmented forest  
73 within Bawangling National Nature Reserve (BNNR), Hainan, China [Turvey et al.,  
74 2015]. Despite formal protection measures and an apparently normal birth rate  
75 [Fellowes et al., 2008], since 1989 this population has fluctuated between 15–25  
76 gibbons and has shown no consistent growth for several decades [Bryant, 2014;  
77 Turvey et al., 2015]. The small size of this population raises serious concerns for  
78 long-term survival of the species, and tailored conservation actions are urgently  
79 required.

80 To date, the evidence base for the Hainan gibbon has been limited, with a lack of  
81 systematically-derived information precluding accurate understanding of the species'  
82 behavior, biology and ecology [Bryant, 2014; Turvey et al., 2015]. This data  
83 limitation has constrained conservation planning by preventing identification of  
84 necessary tailored management actions. As long-term successful recovery will likely  
85 require intensive, carefully planned and co-ordinated management to conserve and  
86 expand this remnant population, it is crucial to identify key ecological characteristics  
87 and life history traits, such as annual and seasonal home range size, interbirth interval  
88 and age at first reproduction, that may be regulating gibbon population growth.

89 The Hainan gibbon reportedly exhibits the largest home range of any gibbon species  
90 [Chan et al., 2005], with estimates ranging from 2 km<sup>2</sup> to nearly 10 km<sup>2</sup> [Liu et al.,  
91 1989, 1995; Liu and Tan, 1990; Zhou et al., 2008a, 2008b]. In most cases, past  
92 studies describing Hainan gibbon ranging requirements have failed to report either  
93 detailed sampling protocol/effort or statistical analyses employed when estimating  
94 home range area. However, the large home range estimate reported in the most recent  
95 published study [Zhou et al., 2008a] (see Table 1) is derived from an extended multi-  
96 year sampling period (2002–2006), which may have overestimated home range size  
97 by capturing yearly shift in home range position, producing a conflated estimate. By  
98 comparison, other *Nomascus* species have home range estimates ranging from 0.40–  
99 1.51 km<sup>2</sup> (usually based on multiple groups studied over individual sampling periods  
100 of several months) [Fan and Jiang, 2008a; Fan et al., 2010; Fei et al., 2012], and other  
101 gibbon genera typically have home ranges of 0.20–0.88 km<sup>2</sup> [Chivers et al., 2013]  
102 (Supporting Information, Table S1). Such large differences (up to a fiftyfold  
103 difference) in home range area among species of the same genus are not common in  
104 other primate taxa (e.g., *Cercopithecus*, *Colobus*, *Hapalemur*, *Lemur*, *Papio*,

105 *Propithecus* [Clutton-Brock and Harvey, 1977; Tan, 1999]), so that this substantial  
106 difference in spatial requirements between the Hainan gibbon and other crested  
107 gibbons seems unlikely.

108 However, a large home range area for the last Hainan gibbon population may be the  
109 result of specific ecological conditions at BNNR. This population persists in  
110 relatively high-elevation forests (800–1200 metres above sea level (m asl)) that may  
111 represent suboptimal habitat with reduced food-tree availability, requiring gibbons to  
112 travel longer distances for food [Liu et al., 1989; Chan et al., 2005; Zhou et al.,  
113 2008b]. Low population density also may facilitate home range expansion, as few  
114 neighboring groups exist to restrict range extent through territorial exclusion  
115 [Fellowes et al., 2008]. Studies of other primate species such as blue monkey  
116 (*Cercopithecus mitis*) and indri (*Indri indri*) indicate an increase in home range area  
117 for groups inhabiting areas of low population density [Butynski, 1990; Glessner and  
118 Britt, 2005]. The Hainan gibbon's large observed group sizes (mean =  $7 \pm 2.31$ , range  
119 = 3–11 individuals), compared even to other *Nomascus* species (mean =  $5 \pm 1.04$ ,  
120 range = 3–6 individuals [Jiang and Wang, 1999; Fan and Jiang, 2010; Fan et al., 2010;  
121 Chivers et al. 2013]), and polygynous mating system (only observed consistently in  
122 two other *Nomascus* species, *N. concolor* and *N. nasutus* [Fan and Jiang, 2010; Fei et  
123 al., 2012]), may result from the reportedly very large home ranges permitting  
124 acquisition of sufficient resources to support more individuals within groups [Jiang et  
125 al., 1999]. Indeed, Bryant et al. [2015] assessed patterns across all gibbon genera and  
126 found evidence for increased gibbon home range size associated with low group  
127 density in combination with a polygynous mating system and larger group sizes.

128 Gibbons typically tolerate little range overlap (approximately 12–30 %) between  
129 groups [Reichard and Sommer, 1997; Bartlett, 2009; Cheyne et al., 2008; Fei et al.,  
130 2012]. The Hainan gibbon's apparently large spatial requirements may therefore be  
131 an important factor regulating the number of groups within BNNR's fragmented  
132 forest, where gibbons are restricted to an area which measures only c. 15 km<sup>2</sup> [Turvey  
133 et al., 2015]. The lack of suitable vacant habitat may force individuals to remain  
134 within natal groups rather than establishing new territories [Zhou et al., 2008b]. In  
135 their largely descriptive paper, based on daily observational data, Liu et al. [1989]  
136 suggested that by the late 1980s, available habitat for new gibbon groups within  
137 BNNR was virtually absent, with the four groups then present estimated to  
138 collectively occupy a total area of 12 km<sup>2</sup>. Accurate understanding of Hainan gibbon  
139 spatial requirements is therefore vital to determine whether habitat limitation within  
140 BNNR may prevent population recovery.

141 Given that assessments of Hainan gibbon home range requirements are limited by a  
142 general lack of reporting of survey methods, monitoring effort, or analytical  
143 approaches used to derive past estimates [Liu et al., 1989, 1995; Liu and Tan, 1990;  
144 Zhou et al., 2008a, 2008b] (see Table 1), it is difficult to critically evaluate whether  
145 the species has an exceptionally large home range, determine the role that range size  
146 may play in regulating population recovery, or identify ecologically suitable  
147 management actions. A more rigorous and methodologically transparent investigation  
148 of Hainan gibbon home range size, whether and how this may vary with season, and  
149 the amount of home range overlap between neighboring groups, conducted using up-  
150 to-date spatial analysis techniques, represents a conservation priority.



151 To address this priority, we conducted extensive fieldwork in BNNR to re-evaluate  
152 Hainan gibbon spatial ecology. The Hainan gibbon's reduced population size, with  
153 only three social groups existing in BNNR and only one of these habituated to the  
154 presence of human observers, presents a challenge to the collection of new data. For  
155 this and other species of extreme rarity, it is not presently clear what impact limited  
156 ranging data may have on home range estimation, particularly given the array of  
157 estimation techniques now available. Although broad-scale habitat data are available  
158 across Hainan [Zhang et al., 2010], high-resolution systematically derived  
159 environmental data associated with gibbon presence/absence within the BNNR  
160 landscape are not readily available. Building upon previous studies which have  
161 focused on investigating the impact of different analytical approaches on home range  
162 size estimation, irrespective of the availability of underlying ecological or habitat  
163 information [Moland et al., 2011; Pebsworth et al., 2012], we set out to investigate the  
164 effect of data limitation upon home range estimation, and assess whether a consensus  
165 can be reached on Hainan gibbon home range requirements through comparison of  
166 different estimation approaches. We also critically assessed the reliability and  
167 representativeness of our home range estimates by employing multiple evaluation  
168 methods aimed at examining whether our survey effort was sufficient to accurately  
169 estimate home range, whether different estimation techniques reached any spatial  
170 concordance, and which estimation methods were able to accommodate known  
171 ranging constraints for Hainan gibbons.

172 We hypothesized that: (A) Hainan gibbon home range is likely to be smaller than  
173 suggested by previous extremely large estimates. This hypothesis is based on the  
174 assumption that previous estimates have overestimated Hainan gibbon home range  
175 size by capturing yearly shift in home range area but reporting this as a static home

176 range estimate. (B) Hainan gibbon home range area is similar in magnitude to that of  
177 other closely related *Nomascus* gibbons (0.4–1.51 km<sup>2</sup>). (C) Home range overlap  
178 between Hainan gibbon groups is similar to that observed for other *Nomascus*  
179 gibbons. Hypotheses B and C are based on the assumption that for *Nomascus*  
180 gibbons, like other primate taxa, species within the same genus will not generally  
181 show large differences (orders of magnitude) in home range area or overlap. (D) By  
182 comparing different estimates and assessing the influence of sample size on estimate  
183 convergence for each method, we can determine the robustness and representativeness  
184 of our data and identify effective home range estimation approaches where sampling  
185 is limited by species rarity.

186

## 187 **METHODS**

### 188 **Study species and study site**

189 At the time of this study, the sole remaining Hainan gibbon population consisted of  
190 three cohesive social groups ('Group A': one adult male, two adult females, nine  
191 immature offspring; 'Group B': one adult male, one adult female, one post-  
192 reproductive female, four immature offspring; 'Group C': one adult male, two adult  
193 females), together with a small, unknown number of solitary individuals [Bryant,  
194 2014]. Immature Hainan gibbons (infants, juveniles, and subadults) are distinguished  
195 from adults by their size (c. 250 g to 4.5 kg, compared to adults: 7–8 kg) and  
196 infrequent vocalisations, and range in age from new-born infants to approximately  
197 eight years [Liu et al., 1989; Chan et al., 2005]. The species has an interbirth interval  
198 of two years [Zhou et al., 2008b] (rather than three years like most other *Nomascus*  
199 and other gibbon species [Chivers et al., 2013]). The few remaining Hainan gibbon

200 individuals in BNNR constitute the global population for the species, as there are no  
201 captive specimens and no other known wild populations [Chan et al., 2005; Turvey et  
202 al., 2015].

203 BNNR is located at 18°57'–19°11'N, 109°03'–109°17'E, and was established in 1980  
204 to protect the remaining Hainan gibbon population and its habitat. It comprises  
205 almost 300 km<sup>2</sup> in total and straddles two counties (Changjiang and Baisha Li  
206 Autonomous Counties). Vegetation within the reserve consists of lowland and  
207 montane/ravine rainforest and evergreen broadleaf forest [Zhang et al., 2010], but the  
208 remnant gibbon population now appears to be constrained to relatively high elevation  
209 habitat in the Futouling region (Fig. 1) [Chan et al., 2005; Fellowes et al., 2008],  
210 which comprises the core area of the reserve. The climate in BNNR is tropical  
211 seasonal with a mean annual temperature of 21.3 °C (minimum in December with  
212 mean of 15 °C, and maximum in June with mean of 22.5 °C), mean annual rainfall of  
213 1,660 mm, and mean relative humidity of 88.6 % [Chan et al. 2005]. There are two  
214 distinct seasons: the wet season occurs from May to October, and the dry season  
215 occurs from November to April [Liu et al., 1995; Zhang et al., 2010]. Limited  
216 available data suggest that Hainan gibbon mating activities peak in the wet season  
217 [Zhou et al., 2008b], meaning that there may be a seasonal difference in energy  
218 requirements and therefore ranging behavior to meet these needs.

219

## 220 **Data collection**

221 Hainan gibbon ranging data were collected in BNNR for all three existing social  
222 groups during two field seasons: dry season (November 2010-February 2011) and wet  
223 season (June 2011-September 2011). Groups were located by their morning

224 vocalizations or ‘songs’ (peak singing period: 06:00-07:00 am, continuing at  
225 decreasing regularity during morning and afternoon) [Chan et al., 2005]. Eight  
226 previously-established elevated listening posts were used, with post selection based  
227 upon recent sightings, representing a variation of the fixed-point survey method  
228 [Brockelman and Srikosamatara, 1993]. Posts were manned from 05:00 am or earlier  
229 until at least 12:00 pm, and abandoned only if no songs were detected.

230 Once located, groups were tracked on foot and observed from underneath the tree  
231 occupied by the majority of the group, with geographic waypoints, elevation and fix  
232 error logged every 15 minutes using a hand-held GPS (Garmin GPSMap 60CSx).  
233 This sampling frequency balanced the speed of gibbon movement through steep  
234 terrain with desired data resolution, and is appropriate for canopy-dwelling primates  
235 [De Luca et al., 2010]. Simple behavioral observations also were recorded.

236 Groups were tracked for as long as possible; tracking ended when animals were lost  
237 due to ranging speed or unsafe terrain. Mean number of hours that groups were  
238 followed per day was  $2.16 \pm 1.73$  hours. Follows often concluded by mid-afternoon  
239 (13:30-15:00 = 71.43% of the data). We assume that between 15:00 to 6:00 am there  
240 is relatively little temporal bias in representation of ranging behavior, as gibbons  
241 typically settle at sleeping sites in the early afternoon [e.g. 12:58-15:00 in *Hylobates*  
242 *lar*: Reichard, 1998; 15:00-17:00 in *N. concolor*: Fan and Jiang, 2008b]. Tracking  
243 sessions lasted for five consecutive days, with sessions for different groups  
244 interspersed in time where possible (e.g., consecutive sessions in a month focusing on  
245 Group A, then B, then C). Observation focused principally on habituated Group B  
246 (63.5 hours), with unhabituated Groups A (just over 1 hour) and C (nearly 11 hours)  
247 more sensitive to human proximity and therefore more difficult to follow.

248 Research conducted within this study complied with protocols approved by the  
249 Hainan Forestry Bureau and the Hainan Provincial Government, and adhered to the  
250 legal requirements of the People's Republic of China and to the American Society of  
251 Primatologists' Principles for the Ethical Treatment of Non Human Primates. Project  
252 design was also approved by the Zoological Society of London's Ethics Committee.

253

#### 254 **Home range estimation**

255 There is no consensus regarding 'best' methods for estimating home range [Walter et  
256 al., 2011]; different estimates provide different information about space use and  
257 estimate reliability [Harris et al., 1990; Grueter et al., 2009]. We therefore employed  
258 multiple computational approaches [Huck et al., 2008; Moland et al., 2011].

259 Estimates were calculated for each group, and seasonal estimates were calculated for  
260 Group B, using four methods: Minimum Convex Polygon (MCP) [Mohr, 1947];  
261 Kernel Density Estimation (KDE) [Worton, 1989], using least-squares cross-  
262 validation (LSCV) [Bowman, 1984] and PLUGIN [Wand and Jones, 1994]; Local  
263 Convex Hull (LoCoH) [Getz et al., 2007], using fixed ( $k$ ) and adaptive ( $a$ ) number of  
264 nearest neighbors [optimal values identified using minimum spurious hole covering  
265 (MSHC) rule; Getz and Wilmers, 2004]; and Brownian Bridge Movement Model  
266 (BBMM) [Horne et al., 2007].

267 MCP and KDE represent the most widely used measures of home range area  
268 [Wartmann et al., 2010; Moland et al., 2011] but are biased by their sensitivity to  
269 outlying points and inability to exclude unused areas inside range boundaries [Börger  
270 et al., 2006; Getz et al., 2007]. LoCoH may provide more accurate estimates due to  
271 the fact that it minimizes the inclusion of areas outside true range boundaries and can

272 allow for interior holes [Huck et al., 2008; Lichti and Swihart, 2011]. BBMM makes  
273 conservative assumptions about space use by incorporating data on an animal's  
274 trajectory of movement between successive locations, and so is less likely to include  
275 areas bound within recorded locations but not actually used [Horne et al., 2007]. Two  
276 smoothing parameters,  $\sigma_1$  (describing distance from line joining two locations  
277 travelled during one time-step) and  $\sigma_2$  (related to imprecision of recorded locations)  
278 were used in the BBMM computation to incorporate movement trajectory uncertainty.  
279 We estimated  $\sigma_1$  using Horne et al.'s [2007] maximum log-likelihood algorithm, and  
280 set  $\sigma_2$  to equal the estimated accuracy of recorded locations, defined as the inherent  
281 GPS device accuracy plus average location fix error. BBMM was only used to assess  
282 Group B's range, as this was the only group for which we could collect successive  
283 locations and extensive movement data.

284 MCP estimates were calculated using Hawth's Analysis Tools V.3.27 [Beyer, 2004]  
285 within ArcMap V.10.0 [ESRI, 1999-2010]; KDE estimates were calculated using  
286 Geospatial Modelling Environment V.0.7.1.0 [Beyer, 2012]; and LoCoH and BBMM  
287 estimates were computed using the "adehabitat" package in R V.2.15.1 [Calenge,  
288 2006]. Our dataset contained significant autocorrelation (Schoener indices  $<1.6$  or  
289  $>2.4$ ; Swihart and Slade indices  $>0.6$ ); home range may actually be best represented  
290 by autocorrelated observations [De Solla et al., 1999; Valcu and Kempnaers, 2010],  
291 so subsampling was not performed as it may remove biological signals such as animal  
292 movement patterns driven by underlying ecological processes (e.g., altitude,  
293 vegetation/prey/predator distributions) and increase imprecision [Dray et al., 2010].  
294 Appropriate estimate-specific density isopleths were employed for estimate  
295 comparison.

296 Estimate variation was assessed by calculating absolute and relative differences in  
297 area, and ‘minimum agreed area of use’ (minimum between-estimate spatial overlap).  
298 To avoid biasing results with multiple estimate variants, we only included data for  
299 MCP, KDE-PLUGIN, a-LoCoH and BBMM, based upon preliminary assessment of  
300 the performance of different KDE and LoCoH estimates against the underlying  
301 location distribution. Overlaps were computed in ArcMap V.10.0.

302 To investigate temporal partitioning of Group B’s yearly home range, we analysed  
303 seasonal home range variation, determining overlap between seasonal estimates from  
304 each method and comparing this to the larger seasonal estimate and relevant yearly  
305 estimate. We also determined overlap between different group estimates. Analysis  
306 was conducted in ArcMap V.10.0.

307

### 308 **Estimate reliability and performance**

309 To examine whether survey effort was sufficient to capture home ranges, we  
310 calculated the stepwise increase in MCP area with each position fix as the proportion  
311 of total estimated MCP area/group. We conducted Incremental Area Analysis (IAA)  
312 [Kenward and Hodder, 1996] using ABODE [Laver, 2005] in ArcMap V.10.0, with  
313 random subsampling of locations, and produced MCPs for incremental datasets. To  
314 investigate whether range estimates reached a plateau with increasing data, we  
315 assessed IAA curves against two regression models, a simple linear model and a two-  
316 parameter asymptotic exponential model passing through the origin, in R V.2.15.1 [R  
317 Development Core Team, 2012]; further exponential models not constrained to the  
318 origin were not considered, as we would expect zero data-points to report a home  
319 range estimate of zero. The second-order Akaike Information Criterion (AICc)

320 [Hurvich and Tsai, 1989] was computed for each model using “AICcmodavg”  
321 [Mazerolle, 2012] to assess model performance and IAA curve fit. Between-model  
322 discrimination was investigated using ANOVA and comparing ranked models with  
323  $\Delta AIC_c$ , with  $\Delta AIC > 4$  identifying models representing a better fit than the null model  
324 [Burnham and Anderson, 2004]. Model fit was also assessed by checking for  
325 overdispersion; residual deviance was compared to degrees of freedom and tested  
326 against the chi-squared distribution. Formal assessment was conducted for Group B  
327 data only.

328 The extent to which different estimate forms reached spatial concordance for areas  
329 utilized by each group was measured for group estimates and seasonal Group B  
330 estimates. Concordance between estimate pairs was determined by comparing spatial  
331 overlap in ArcMap V.10.0, expressed as relative percentage overlap against the larger  
332 of the two estimates.

333 Within BNNR, areas above 1,200 m asl in elevation are considered floristically  
334 unsuitable for Hainan gibbons [Liu and Tan, 1990], and areas below 800 m asl are  
335 largely unsuitable as primary vegetation is generally absent [Chan et al., 2005]. We  
336 assessed estimate reliability by investigating their ability to exclude areas that gibbons  
337 are unlikely to utilize. We extracted elevation contours from high-resolution (1-arc-  
338 second/30 m) Advanced Spaceborne Thermal Emission and Reflection Radiometer  
339 Global DEM V.2 [NASA/METI, 2011], using a circular neighborhood focal statistic  
340 with one-cell search radius to resample DEM data. We generated a 10 m-interval  
341 contour dataset, assessing accuracy by comparison with elevations recorded by GPS  
342 for 12 key BNNR features; differences between GPS-described elevations and DEM-  
343 derived contours nearest each feature were minimal (average difference = 15.5 m).  
344 Areas in BNNR above 1,200 m asl and below 800 m asl were then identified as



345 expected holes within Group B estimates, with estimate performance visually  
346 assessed against these areas. Analyses were conducted in ArcMap V.10.0.

347

## 348 **RESULTS**

### 349 **Home range size**

350 Home range estimates are based on 75.5 hours of observations from 35 contact days,  
351 over 93 field-days across both field seasons (Supporting Information, Table S2). We  
352 successfully encountered gibbons on 41% of field days, yielding a dataset of 248  
353 locations (Group A: 10 locations, Group B: 208 locations, Group C: 30 locations).  
354 Gibbon groups occupied distinct areas of BNNR during the study (Fig. 1). Behavior  
355 observed during tracking was typical of daily gibbon activity patterns (Supporting  
356 Information, Text S1, Tables S3-S4, Fig. S1).

357 Estimation techniques produced varying home range values. Group B's yearly home  
358 range was estimated at 1.28–1.92 km<sup>2</sup> (Fig. 2). Seasonal ranges generally appear  
359 smaller, with dry season range estimated at 0.72–1.38 km<sup>2</sup>, although a generous upper  
360 estimate provided by the KDE h-LSCV method produced greater variation for the  
361 group's wet season range at 0.66–2.27 km<sup>2</sup>. Group A's range was estimated at 0.15–  
362 2.54 km<sup>2</sup> using a small dataset sampled across both seasons; Group C's range was  
363 estimated at 0.06–0.20 km<sup>2</sup> based on wet season data only (Table 2).

364 KDE h-LSCV generally produced the largest estimates, and in one case provided a  
365 seasonal estimate for Group B that was larger than the annual estimate for this group  
366 (Fig. 2), a counterintuitive result that is likely due to the inability of this bandwidth  
367 estimator to deal with dispersed (rather than clustered) underlying geographic points,

368 meaning this method may have slightly overestimated the wet season home range for  
369 Group B. BBMM also generated large estimates for Group B. while LoCoH  
370 estimates were most conservative (Table 2). Regardless, Group B between-estimate  
371 variation was relatively low (smallest and largest yearly estimates, 33% difference);  
372 greater between-estimate variation was apparent in smaller datasets and was greatest  
373 for Group A, for which fewest data were available (smallest and largest estimates, c.  
374 94% difference), although variation for Group C estimates and Group B's wet season  
375 estimates was similar (c. 70% difference). The minimum agreed area indicated by all  
376 estimates for Group B's yearly home range was c. 1 km<sup>2</sup>, and closer to 0.5 km<sup>2</sup> for  
377 seasonal ranges; Group A's minimum agreed area was equivalent to this group's  
378 smallest estimate (a-LoCoH), and Group C's was close to this group's smallest  
379 estimate (k-LoCoH) (Table 2; Supporting Information, Fig. S2-6).

380 Group B's home range appears slightly larger in the wet season relative to the dry  
381 season, based on median seasonal estimates (Table 2; Fig. 2). Geographic polygons  
382 for KDE h-PLUGIN and LoCoH indicate this group seasonally utilizes different areas  
383 of yearly home range (Supporting Information, Fig. S2-4), although this is not  
384 reported by other estimates. Seasonal range overlap indicated by MCP, KDE h-LSCV  
385 and BBMM was greater (0.85–1.20 km<sup>2</sup>, or 53–61% of larger estimate; Table 3) than  
386 for KDE h-PLUGIN and LoCoH (0.17–0.57 km<sup>2</sup>, or 24–48% of larger estimate),  
387 suggesting greater seasonal partitioning. Proportion of yearly home range utilized all  
388 year was 54–65% based on MCP, KDE h-LSCV and BBMM, but 13.3–38.6% based  
389 on KDE h-PLUGIN and LoCoH. A median value suggests 0.71 km<sup>2</sup> (c. 50% of  
390 yearly home range) is used in both seasons.

391 Group overlap was directly observed on one occasion during fieldwork, when Group  
392 A was observed at the edge of the area usually occupied by Group C, while Group C

393 was simultaneously tracked and observed elsewhere in its range. Actual estimated  
394 group overlap was dependent upon estimation method. MCP, k-LoCoH and a-LoCoH  
395 indicated extremely little (<0.15%) or no overlap. KDE-LSV and KDE-PLUGIN  
396 estimated overlap of 0.09–0.32 km<sup>2</sup> for Groups A and B, representing 6–17% of these  
397 groups' home range. Overlap between Groups A and C was much smaller (c. 0.07  
398 km<sup>2</sup>), although this corresponds to 3–43% of these groups' home ranges due to large  
399 difference in size and greater estimate uncertainty for these groups. Groups B and C  
400 were never observed in similar locations, so no overlap was estimated.

401

#### 402 **Estimate reliability and performance**

403 IAA curves for Group B's yearly and seasonal datasets show MCP estimates  
404 plateauing with increasing number of locations (Supporting Information, Fig. S7-9);  
405 regression analysis confirmed the asymptotic nature of all datasets. No regression  
406 models showed overdispersion (probability of observed residual deviance > 0.995 for  
407 all models); models were significantly different from each other for yearly and  
408 seasonal datasets (all ANOVAs,  $P < 0.001$ ), and exponential model terms were  
409 significant for all curves (all ANOVAs,  $P < 0.001$ , parameter estimates each >2 S.E.  
410 difference), indicating model simplification was not justified and curves are better  
411 described by exponential models than linear models. The exponential model  
412 indicated that yearly range estimates for Group B stabilize and converge at 110  
413 locations (asymptote 'Asym' =  $1.50 \pm 0.010$ , rate constant 'lrc' =  $-2.91 \pm 0.040$ ,  $n =$   
414 208), wet season estimates at 100 locations (Asym =  $1.51 \pm 0.010$  and lrc =  $-3.00 \pm$   
415  $0.026$ ,  $n = 102$ ), and dry season estimates at 90 locations (Asym =  $0.82 \pm 0.009$ , lrc =  
416  $-2.43 \pm 0.062$ ,  $n = 106$ ) (Supporting Information, Fig. S7-9). Estimates derived from

417 Group B datasets are therefore considered representative of this group's spatial  
418 requirements.

419 Group B estimate concordance was generally good, with pair-wise yearly  
420 comparisons showing more than 50% spatial overlap, and almost half showing 75%  
421 overlap or more (Table 4; Supporting Information, Fig. S2–4). Concordance was  
422 greatest between variants of the same method, or estimates generated utilizing similar  
423 computational approaches (78% overlap between KDE variants; 95% between  
424 LoCoH variants; >80% between MCP and LoCoH), although estimates from different  
425 approaches showed similar concordance (MCP and KDE overlap, and KDE h-LSCV  
426 and BBMM overlap, all  $\geq 75\%$ ). Group B's dry season estimates showed similar  
427 patterns, with estimate-variant comparisons and MCP-LoCoH comparisons showing  
428 80% or greater concordance, and comparison between BBMM and MCP and KDE  
429 variants showing 77% or greater concordance; conversely, for wet season estimates  
430 almost half of pair-wise estimate comparisons showed less than 50% overlap, and  
431 only MCP and BBMM estimates showed more than 75% overlap (Supporting  
432 Information, Tables S5–6). As expected, concordance of Group A and C estimates  
433 was worse, with overlap typically 50% or less, and only estimate-variant comparisons  
434 showing substantial overlap (e.g. 62% between Group A KDE variants, 92% between  
435 Group C KDE variants, 72% between Group C LoCoH variants; data not shown).

436 Group B yearly LoCoH estimates produced polygons occurring entirely above 800 m  
437 asl and with clear holes corresponding approximately to areas above 1,200 m asl (Fig.  
438 3a-b); lack of exact concordance may result from slightly imprecise methods for  
439 generating elevation contours, or model assumptions about space between locations.

440 Seasonal LoCoH polygons also excluded lower-elevation and higher-elevation areas

441 and incorporated reciprocal areas to the east and west sides of holes, with a-LoCoH  
442 slightly better at excluding higher-elevation areas (Fig. 3c-f). Other methods  
443 generally failed to exclude higher-elevation areas, instead assuming that gaps  
444 indicated by LoCoH were within the home range, accounting for larger estimates  
445 reported by these methods. LoCoH estimates can therefore be regarded as the most  
446 reliable Hainan gibbon home range estimates.

447

## 448 **DISCUSSION**

449 This study represents the most robust investigation of Hainan gibbon spatial  
450 requirements to date. Our analyses indicate a yearly home range of 1–2 km<sup>2</sup> for  
451 Group B, with 1.49 km<sup>2</sup> closest to the median of all estimates for this group. Using  
452 multiple approaches, we demonstrate that our ranging data for Group B are  
453 representative, and that methodologically transparent estimates derived from these  
454 data constitute a robust representation of Hainan gibbon home range. These data  
455 reveal that Hainan gibbon spatial requirements are much smaller than previous  
456 estimates used to explain the species' limited population growth [Zhou et al., 2008a,  
457 2008b], which substantially overestimated Hainan gibbon home range.

458 Whereas our revised estimate is much lower than those from previous studies, it is  
459 still relatively large for a gibbon home range. However, it is comparable to estimates  
460 for some other *Nomascus* gibbons. Estimates of 1.3 km<sup>2</sup> for Cao Vit gibbon (*N.*  
461 *nasutus*) [Fan et al., 2010; Fei et al., 2012] and 1.51 km<sup>2</sup> for black crested gibbon (*N.*  
462 *concolor*) in Wuliangshan, China [Fan and Jiang, 2008a] are similar to our estimates.  
463 These comparisons are particularly relevant, because these species are considered  
464 phylogenetically closest to *N. hainanus* [Thinh et al., 2010], which may suggest that

465 large ranges may be an evolutionary characteristic for these taxa. These estimates  
466 also are derived from small, Critically Endangered populations with limited, poor-  
467 quality habitat [Jiang et al., 2006; Fan and Jiang, 2008a]. Other *Nomascus* species  
468 occurring in better-quality habitat have similar sized home ranges [*N. siki*: 0.38 km<sup>2</sup>,  
469 Rowe and Myers, 2011; *N. leucogenys*: 0.40 km<sup>2</sup>, Julia Ruppell, pers. comm. April  
470 2013; *N. gabriellae*: 0.60 km<sup>2</sup>, Marina Kenyon, pers. comm. April 2013] to other  
471 gibbon genera [typically 0.20–0.88 km<sup>2</sup>, Chivers et al., 2013]. Larger home ranges of  
472 Critically Endangered *Nomascus* gibbons may therefore represent a response to  
473 suboptimal conditions rather than an intrinsic trait [Bryant et al., 2015].

474 Group B uses c. 50% of its yearly range in both seasons, with evidence of seasonal  
475 utilization of different areas, and slightly larger overall wet season home range  
476 relative to that utilized in the dry season. Such differences could reflect seasonal  
477 variation in food availability, as seen in other gibbons (e.g., *Hylobates lar* and  
478 *Symphalangus syndactylus*), which can reduce range area during times of low food  
479 abundance by accepting lower quality food and/or a lower diversity of food types  
480 [Raemaekers, 1980]. Seasonal variation in food availability in BNNR is incompletely  
481 understood, but February-April (late dry season) may be the most food-limited period  
482 [Chan et al., 2005], suggesting Hainan gibbons may adopt similar behavior at BNNR  
483 to *H. lar* and *S. syndactylus* in Malaysian lowland tropical forests.

484 Hainan gibbon ranging behavior is likely influenced by landscape features, including  
485 physical attributes (e.g., food-tree distribution), and anthropogenic landscape  
486 modification/disturbance (e.g., roads, agricultural incursion, deforestation). LoCoH  
487 estimates excluded elevations above 1,200 m from Hainan gibbon home range  
488 estimates and confirmed that only areas above 800 m were utilized. This supports

489 previous reports of Hainan gibbon preference for forest between these elevations,  
490 providing some evidence for elevation as a determinant of home range use.  
491 Unfortunately we could not obtain sufficiently high-resolution data on other landscape  
492 features to assess the effect that these may have upon gibbon space use. Therefore, a  
493 crucial next step is to relate observed gibbon ranging patterns to underlying habitat  
494 quality and structure across BNNR, to identify ecological drivers of space use, and  
495 permit more fine-grained assessment of management requirements and priorities to  
496 enhance the BNNR landscape to support gibbons. However, our study provides an  
497 essential first step towards this conservation goal. In addition, an understanding of  
498 the predictors of ranging behavior is vital to assess potential habitat suitability outside  
499 areas of current gibbon distribution when considering possible future intensive  
500 management actions.

501 Sample size, sampling duration, and computational technique all affected home range  
502 estimates. Problems of reduced sample size are clear in estimates for unhabituated  
503 groups A and C, which are based upon modest datasets and show considerable  
504 variation and poor geographic concordance; IAA results suggest these datasets are  
505 unlikely to be representative. Group B range estimates also varied, from 71.1%  
506 difference for wet season estimates ( $n = 102$ ) to 46.7% for dry season estimates ( $n =$   
507 106) and 33% for yearly estimates ( $n = 208$ ). Yearly data show greatest spatial  
508 concordance, indicating that different estimators converge upon range extent and  
509 distribution as more locations are included. The influence of sample size and  
510 estimation technique on home range estimates for mammals are well-documented  
511 [Harris et al., 1990; Boyle et al., 2009; Grueter et al., 2009]. Home range estimation  
512 is therefore explicit to a given definition, technique and sample, making it vital to  
513 report methods in full for future investigations of Hainan gibbon spatial ecology.

514 However, we have demonstrated that it is possible to derive home range estimates that  
515 are robust and representative for species of extreme rarity, despite data collection  
516 being especially challenging, by using multiple estimation metrics and investigating  
517 their concordance and ability to cope with known spatial barriers (physical or  
518 ecological) that affect animal movement.

519 Seasonal differences detected in Group B range size and location also indicate that  
520 specifying the temporal scale of data collection is crucial in home range estimation.  
521 Effects of sampling duration on home range estimation remain largely unexplored  
522 compared to sampling frequency and sample size [although see Moland et al., 2011].  
523 We have been explicit about sampling protocol and effort (duration, observation  
524 success rate) that produced locational datasets. Past studies describing Hainan gibbon  
525 ranging requirements generally failed to report one (or all) of these parameters, and  
526 often crucially the method employed for estimating range. For example, Liu and Tan  
527 [1990] reported an observation frequency of 10 days/month during their year-long  
528 study, but did not detail location collection frequency, observation success rate,  
529 sample size or computational approach used to derive their estimate of 2–5 km<sup>2</sup>. The  
530 largest reported estimates [5.48–9.87 km<sup>2</sup>; Fellowes et al., 2008; Zhou et al., 2008a]  
531 likely represent a conflation of range size and range shift over time. These estimates  
532 are reportedly based upon 220 observation days between 2002-2006 [Zhou et al.,  
533 2008a], but frequency and duration of location collection and method for deriving  
534 estimates are not reported. These estimates may have captured changing space use  
535 patterns between successive years, leading to overestimation of spatial requirements.  
536 Conversely, our estimates, based upon data from 93 days across c.12 months, are  
537 directly comparable to those for *N. concolor* in Wuliangshan based upon 125 days  
538 over 14 months [Fan and Jiang, 2008a], and for *N. nasutus* based upon data from



539 September 2008-December 2009 [Fan et al., 2010]. Controlling for sampling duration  
540 reveals the Hainan gibbon does not have extraordinary spatial requirements compared  
541 to closely related species in similar ecological contexts.

542 Our more modest Hainan gibbon spatial requirements have direct conservation  
543 implications for the last surviving population of this species. Areas of suitable gibbon  
544 habitat are typically saturated with social groups with closely interlocking home  
545 ranges [Reichard and Sommer, 1997], and accurate determination of home range and  
546 overlap are crucial to understanding the capacity of available BNNR habitat to  
547 support multiple groups. Using the previous home range estimate of 9.9 km<sup>2</sup> [Zhou et  
548 al., 2008a, 2008b] and assuming average group size of 6.33 [J. Bryant, pers. obs.  
549 August 2011; BNNR Management Office, pers. comm. January 2016] and 17%  
550 overlap, 15 km<sup>2</sup> of habitat will support 1.8 groups and 11.6 gibbons, suggesting that  
551 available habitat in BNNR is already saturated. However, this is unlikely, as the  
552 population has reportedly comprised 24 or more individuals since 2009 [BNNR  
553 Management Office, pers. comm. January 2016]. Conversely, for an exclusive group  
554 range of 1.25 km<sup>2</sup> (1.5 km<sup>2</sup> excluding 17% overlap), 15 km<sup>2</sup> could support 76 gibbons  
555 in 12 groups. Home range and habitat availability may therefore be less important  
556 than supposed in constraining population growth, which may instead be regulated by  
557 other factors (e.g., genetic relatedness, life history traits such as age at first  
558 reproduction, mate availability, human disturbance), although we recognize that other  
559 habitat features (e.g., variable habitat quality/suitability) may impact the population.  
560 Preventing further habitat degradation and enhancing/increasing available habitat  
561 remain crucial to survival of gibbons and other species in BNNR, and substantial  
562 habitat increase is required for the population to thrive instead of just survive.  
563 However, our new robust baseline on Hainan gibbon spatial requirements, and

564 clarification of the potential influence of home range on gibbon population dynamics,  
565 indicate that attention should now be directed to assessing the role of other ecological  
566 or anthropogenic factors that may also constrain gibbon population growth. More  
567 broadly, our study also demonstrates the value of deriving and comparing multiple  
568 home range metrics when faced with limited sample sizes or challenges to data  
569 collection, as is often the case with species of extreme rarity. Moving forward, given  
570 the current biodiversity extinction crisis and increase in species rarity across taxa and  
571 around the globe, the methodological insights gained from this work will therefore  
572 have increasing relevance and applicability.

573

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589

590 **REFERENCES**

591 Baillie JEM, Butcher ER. 2012. Priceless or Worthless? The World's Most

592 Threatened Species. London: Zoological Society of London. 123p.

593 Bartlett TQ. 2009. The Gibbons of Khao Yai: Seasonal Variation in Behavior and

594 Ecology. New Jersey: Pearson Prentice Hall. 170 p.

595 Beyer HL. 2004. Hawth's analysis tools for ArcGIS (2002-2006), V.3.27. Available

596 at: <http://www.spatial ecology.com/htools> (last accessed 16 July 2014).

597 Beyer HL. 2012. Geospatial modelling environment (V.0.7.2.0). Available at:

598 <http://www.spatial ecology.com/gme> (last accessed 16 July 2014).

599 Börger L, Francon N, De Michele G, et al. .2006. Effects of sampling regime on the

600 mean and variance of home range size estimates. *Journal of Animal Ecology*

601 75:1393–1405.

602 Bowman AW. 1984. An alternative method of cross-validation for the smoothing of

603 density estimates. *Biometrika* 71:353–360.

604 Boyle SA, Lourenço WC, da Silva LR, Smith AT. 2009. Home range estimates vary

605 with sample size and methods. *Folia Primatologica* 80:33–42.

606 Brockelman WY, Srikosamatara S. 1993. Estimation of density of gibbon groups by

607 use of loud songs. *American Journal of Primatology* 29:93–108.

608 Bryant JV. 2014. Developing a Conservation Evidence-Base for the Critically

609 Endangered Hainan Gibbon (*Nomascus hainanus*). PhD thesis. University College

610 London/Zoological Society of London, London.

611 Bryant JV, Olson VA, Chatterjee HJ, Turvey ST. 2015. Identifying environmental  
612 versus phylogenetic correlates of behavioural ecology in gibbons: implications for  
613 conservation management of the world's rarest ape. *BMC Evolutionary Biology*  
614 15:171–183.

615 Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and  
616 BIC in model selection. *Sociological Methods & Research* 33:261–304.

617 Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in  
618 high- and low-density subpopulations. *Ecological Monographs* 60:1–26.

619 Calenge C. 2006. The package “adehabitat” for the R software: a tool for the analysis  
620 of space and habitat use by animals. *Ecological Modelling* 197:516–519.

621 Chan BPL, Fellowes JR, Geissmann T, Zhang J. 2005. Hainan gibbon status survey  
622 and conservation action plan. Hong Kong: Kadoorie Farm & Botanic Garden.

623 Cheyne SM, Thompson CJH, Phillips AC, Hill RMC, Limin SH. 2008. Density and  
624 population estimate of gibbons (*Hylobates albibarbis*) in the Sabangau catchment,  
625 Central Kalimantan, Indonesia. *Primates* 49:50–56.

626 Chivers DJ, Anandam MV, Groves CP, et al. 2013. Family Hylobatidae (gibbons). In:  
627 Mittermeier RA, Rylands AB, Wilson DE, editors. *Handbook of the mammals of*  
628 *the world. Volume 3: primates*. Barcelona: Lynx Edicions. p 754–791.

629 Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization.  
630 *Journal of Zoology* 183:1–39.

631 De Luca DW, Picton Phillipps G, Machaga SJ, Davenport TRB. 2010. Home range,  
632 core areas and movement in the Critically Endangered kipunji (*Rungwecebus*  
633 *kipunji*) in southwest Tanzania. *African Journal of Ecology* 48:895–904.

634 De Solla SR, Bonduriansky R, Brooks RJ. 1999. Eliminating autocorrelation reduces  
635 biological relevance of home range estimates. *Journal of Animal Ecology* 68:221–  
636 234.

637 Dray S, Royer-Carenzi M, Calenge C. 2010. The exploratory analysis of  
638 autocorrelation in animal-movement studies. *Ecological Research* 25:673–681.

639 ESRI. 1999-2010. ArcMap 10.0, ArcGIS desktop 10 service pack 4. Redlands, CA:  
640 Environmental Systems Research Institute.

641 Fan P, Fei H, Xiang Z, et al. 2010. Social structure and group dynamics of the Cao Vit  
642 gibbon (*Nomascus nasutus*) in Bangliang, Jingxi, China. *Folia Primatologica*  
643 81:245–253.

644 Fan P, Jiang X. 2008a. Effects of food and topography on ranging behavior of black  
645 crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountain, Yunnan,  
646 China. *American Journal of Primatology* 70:871–878.

647 Fan P, Jiang X. 2008b. Sleeping sites, sleeping trees, and sleep-related behaviors of  
648 black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, central  
649 Yunnan, China. *American Journal of Primatology* 70:153–160.

650 Fan P, Jiang X. 2010. Maintenance of multifemale social organization in a group of  
651 *Nomascus concolor* at Wuliang Mountain, Yunnan, China. *International Journal of*  
652 *Primatology* 31:1–13.

653 Fei H, Scott MB, Zhang W, et al. 2012. Sleeping tree selection of Cao Vit gibbon  
654 (*Nomascus nasutus*) living in degraded karst forest in Bangliang, Jingxi, China.  
655 *American Journal of Primatology* 74:998–1005.

656 Fellowes JR, Chan BPL, Zhou J, Chen S, Yang S. 2008. Current status of the Hainan  
657 gibbon (*Nomascus hainanus*): progress of population monitoring and other priority  
658 actions. *Asian Primates Journal* 1:2–9.

659 Getz WM, Fortmann-Roe S, Cross PC, et al. 2007. LoCoH: nonparametric kernel  
660 methods for constructing home ranges and utilization distributions. PLoS ONE  
661 2:e207.

662 Getz WM, Wilmers CC. 2004. A local nearest-neighbor convex-hull construction of  
663 home ranges and utilization distributions. *Ecography* 27:489–505.

664 Glessner KDG, Britt A. 2005. Population density and home range size of *Indri indri*  
665 in a protected low altitude rain forest. *International Journal of Primatology* 26:855–  
666 872.

667 Groombridge JJ, Massey JG, Bruch JC, et al. 2004. An attempt to recover the po’ouli  
668 by translocation and an appraisal of recovery strategy for bird species of extreme  
669 rarity. *Biological Conservation* 118:365–375.

670 Grueter CC, Li D, Ren B, Wei F. 2009. Choice of analytical method can have  
671 dramatic effects on primate home range estimates. *Primates* 50:81–84.

672 Harris S, Cresswell WJ, Forde PG, et al. 1990. Home-range analysis using radio-  
673 tracking data—a review of problems and techniques particularly as applied to the  
674 study of mammals. *Mammal Review* 20:97–123.

675 Horne JS, Garton EO, Krone SM, Lewis JS. 2007. Analyzing animal movements  
676 using Brownian bridges. *Ecology* 88:2354–2363.

677 Huck M, Davison J, Roper TJ. 2008. Comparison of two sampling protocols and four  
678 home-range estimators using radio-tracking data from urban badgers *Meles meles*.  
679 *Wildlife Biology* 14:467–477.

680 Hurvich CM, Tsai CL. 1989. Regression and time series model selection in small  
681 samples. *Biometrika* 76:297–307.

682 Jiang X, Luo Z, Zhao S, Li R, Liu C. 2006. Status and distribution pattern of black  
683 crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountains,  
684 Yunnan, China: implication for conservation. *Primates* 47:264–271.

685 Jiang X, Wang Y, Wang Q. 1999. Coexistence of monogamy and polygyny in black-  
686 crested gibbon (*Hylobates concolor*). *Primates* 40:607–611.

687 Kenward RE, Hodder KH. 1996. RANGES V: an analysis system for biological  
688 location data. Swindon, UK: Natural Environment Research Council.

689 Laver PN. 2005. ABODE: kernel home range estimation for ArcGIS, using VBA and  
690 ArcObjects. Blacksburg, VA: Department of Fisheries and Wildlife Sciences,  
691 Virginia Tech.

692 Lichti NI, Swihart RK. 2011. Estimating utilization distributions with kernel versus  
693 local convex hull methods. *Journal of Wildlife Management* 75:413–422.

694 Liu X, Liu Z, Chen J, Jiang H. 1995. The home range use and seasonal changes in  
695 Hainan gibbon. *Journal of Sun Yatsen University (Supplement)* 3:168–171.

696 Liu Z, Tan C. 1990. An analysis on habitat structure of the Hainan gibbon. *Acta*  
697 *Theriologica Sinica* 10(3):163–169.

698 Liu Z, Yu S, Yuan X. 1984. Resources of the Hainan black gibbon and its present  
699 situation. *Chinese Wildlife* 6:1–4.

700 Liu Z, Zhang Y, Jiang H, Southwick C. 1989. Population structure of *Hylobates*  
701 *concolor* in Bawanglin Nature Reserve, Hainan, China. *American Journal of*  
702 *Primatology* 19:247–254.

703 Mazerolle MJ. 2012. AICcmodavg: model selection and multimodel inference based  
704 on (Q)AIC(c). R package V.1.26.

705 Mohr CO. 1947. Table of equivalent populations of North American small mammals.  
706 *American Midland Naturalist* 37:223–249.

707 Moland E, Olsen EM, Andvord K, Knutsen JA, Stenseth NC. 2011. Home range of  
708 European lobster (*Homarus gammarus*) in a marine reserve: implications for future  
709 reserve design. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1197–1210.

710 NASA/METI. 2011. Advanced spaceborne thermal emission and reflection  
711 radiometer global digital elevation model, V.2. Sioux Falls, SD: NASA Land  
712 Processes Distributed Active Archive Center (LP DAAC).

713 Pebsworth PA, Morgan HR, Huffman MA. 2012. Evaluating home range techniques:  
714 use of Global Positioning System (GPS) collar data from chacma baboons.  
715 *Primates* 53: 345–355.

716 R Development Core Team. 2012. R: a language and environment for statistical  
717 computing. (V.2.15.1). Vienna, Austria: R Foundation for Statistical Computing.

718 Raemaekers J. 1980. Causes of variation between months in the distance traveled  
719 daily by gibbons. *Folia Primatologica* 34:46–60.

720 Reichard U. 1998. Sleeping sites, sleeping places, and presleep behavior of gibbons  
721 (*Hylobates lar*). *American Journal of Primatology* 46:35–62.

722 Reichard U, Sommer V. 1997. Group encounters in wild gibbons (*Hylobates lar*):  
723 agonism, affiliation, and the concept of infanticide. *Behaviour* 134:1135–1174.

724 Rowe N, Myers M. 2011. All the world's primates. Available at:  
725 [www.alltheworldsprimates.org](http://www.alltheworldsprimates.org) (last accessed 16 July 2014).

726 Schwitzer C, Mittermeier RA, Rylands AB, et al. 2014. *Primates in Peril: The*  
727 *World's 25 Most Endangered Primates 2012–2014*. Arlington, VA: IUCN SSC  
728 Primate Specialist Group, International Primatological Society, Conservation  
729 International, and Bristol Zoological Society. 87 p.

730 Segan DB, Bottrill MC, Baxter PWJ, Possingham HP. 2011. Using conservation  
731 evidence to guide management. *Conservation Biology* 25:200–202.



732 Sutherland WJ, Pullin AS, Dolman PM, Knight TM. 2004. The need for evidence-  
733 based conservation. *Trends in Ecology and Evolution* 19:305–308.

734 Tan CL. 1999. Group composition, home range size, and diet of three sympatric  
735 bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park,  
736 Madagascar. *International Journal of Primatology* 20: 547–566.

737 Think VN, Mootnick AR, Geissmann T, et al. 2010. Mitochondrial evidence for  
738 multiple radiations in the evolutionary history of small apes. *BMC Evolutionary*  
739 *Biology* 10:74.

740 Turvey ST, Traylor-Holzer K, Wong MHG, et al. 2015. *International Conservation*  
741 *Planning Workshop for the Hainan gibbon: Final Report*. London/Apple Valley,  
742 MN: Zoological Society of London, London/IUCN SSC Conservation Breeding  
743 Specialist Group.

744 Valcu M, Kempenaers B. 2010. Is spatial autocorrelation an intrinsic property of  
745 territory size? *Oecologia* 162:609–615.

746 Walter WD, Fischer JW, Baruch-Mordo S, VerCauteren KC. 2011. What is the proper  
747 method to delineate home range of an animal using today's advanced GPS  
748 telemetry systems: the initial step. In: Krejcar O, editor. *Modern telemetry*. Rijeka,  
749 Croatia: InTech. p 249–286.

750 Wand MP, Jones C. 1994. Multivariate plug-in bandwidth selection. *Computational*  
751 *Statistics* 9:97–116.

752 Wartmann F, Purves R, van Schaik C. 2010. Modelling ranging behaviour of female  
753 orang-utans: a case study in Tuanan, central Kalimantan, Indonesia. *Primates*  
754 51:119–130.

755 Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-  
756 range studies. *Ecology* 70:164–168.

757 Zhang M, Fellowes JR, Jiang X, et al. 2010. Degradation of tropical forest in Hainan,  
758 China, 1991-2008: conservation implications for Hainan gibbon (*Nomascus*  
759 *hainanus*). *Biological Conservation* 143:1397–1404.

760 Zhou J, Chan BPL, Wei F. 2008a. Responses to inter-group encounters of the Hainan  
761 gibbon *Nomascus hainanus*. *Zoological Research* 29:667–673.

762 Zhou J, Wei F, Li M, et al. 2005. Hainan black-crested gibbon is headed for  
763 extinction. *International Journal of Primatology* 26:453–465.

764 Zhou J, Wei F, Li M, Chan BPL, Wang D. 2008b. Reproductive characters and  
765 mating behaviour of wild *Nomascus hainanus*. *International Journal of*  
766 *Primatology* 29:1037–1046.

767

768 **Table 1.** Previously reported home range estimates for the Hainan gibbon, with  
769 details of aims, methods, sampling effort and results (home range, km<sup>2</sup>) of each study.

770

771 **Table 2.** Variation in home range estimates and associated metrics for Hainan gibbon  
772 groups, and for Group B seasonal ranges.

773

774 **Table 3.** Group B seasonal range overlap by estimation method.

775

776 **Table 4.** Geographic concordance between Group B yearly home range estimates:  
777 percentage overlap between estimate pairs (calculated against larger of two  
778 estimates), with area of overlap (km<sup>2</sup>) in parentheses. Poor spatial concordance  
779 (<50%) indicated in italics, good concordance (>75%) in bold.

780

781 **Fig. 1.** Location of Hainan gibbon groups in Bawangling National Nature Reserve,  
782 showing: ranging location datasets with Minimum Convex Polygons per group,  
783 relative locations of groups, and key landscape features. Note the single circular  
784 location point for Group A within the cluster of crosses for Group C.

785

786 **Fig. 2.** Group B yearly and seasonal home range estimates (km<sup>2</sup>) by estimation  
787 method.

788

789 **Fig. 3.** Group B yearly (a-b), dry season (c-d) and wet season (e-f) home range k-  
790 LoCoH (a,c,e) and a-LoCoH (b,d,f) estimates, against DEM elevation contours (10 m  
791 intervals). Gaps in LoCoH polygons coincide approximately with elevations of  
792 >1,200 m (red contours); green contours = 800–1,200 m, purple contours <800 m.

Table 1

Study (year/s of data reported)	Aim(s) of study	Methods/Techniques	Effort	Home range size
Liu et al. 1989 (1984–1989)	Preliminary study of ecology and behaviour of remaining Bawangling population	Groups located by morning song bouts, approached and directly observed for individual and social behaviours (for as long as contact could be maintained); no information regarding frequency of location recording or approach/statistics used to determine home range estimate provided	5 days each month	2 km <sup>2</sup> – 5 km <sup>2</sup> (median: 3.5 km <sup>2</sup> )
Liu and Tan 1990 (1984–1985)	Investigate change in abundance, relate gibbon habitat use to vegetation type	Group location and behaviour observed and recorded, along with landscape features; no information regarding how gibbons were located, frequency of location recording, or approach/statistics used to determine home range estimate provided	10 days each month	2 km <sup>2</sup> – 5 km <sup>2</sup> (median: 3.5 km <sup>2</sup> ) Also report: 1–2 km <sup>2</sup> if “mountain ridge forest and peak dwarf forest” are excluded
Liu et al. 1995 (1987–1989)	Quantify home range, habitat choice/use and seasonal patterns	Study area divided into nine zones defined by “vegetation characteristics”; gibbon activity and location (i.e. zone 1-9 only, no geographic coordinates) recorded every 15mins; no information regarding how gibbons were located or approach/statistics used to determine home range estimate provided	160 days total; no information regarding frequency of observations on monthly/yearly scale	3.06 km <sup>2</sup> Also report: “total” home range: 5.0 km <sup>2</sup> (includes areas within range that are not usable due to elevation, habitat type, rainfall etc.)

Zhou et al. 2008a (2002–2006)	Report “inter-group encounters” (interactions between social groups)	Groups located via first morning song, tracked by teams of two and observed until group was lost; no information regarding frequency of location recording or approach/statistics used to determine home range estimate provided	220 days total; 680 hours total	4.38 km <sup>2</sup> – 9.78 km <sup>2</sup>
Zhou et al. 2008b (2002–2006)	Document mating and reproductive behaviours/biology of species (gestation period, interbirth interval etc.)	Groups located via first morning song, tracked by teams of two and observed until group was lost; no information regarding frequency of location recording or approach/statistics used to determine home range estimate provided	Describe a “29-month field study”; 232 days and 548.5 hours total	5.84 km <sup>2</sup> – 9.87 km <sup>2</sup>

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Table 2

Dataset/ Group	Smallest estimate (km <sup>2</sup> )	Largest estimate (km <sup>2</sup> )	Absolute difference (km <sup>2</sup> )	Relative difference (%)	Median of estimates (km <sup>2</sup> )	Estimate closest to median (km <sup>2</sup> )	'Minimum agreed area' (km <sup>2</sup> )
<b>B</b>	a-LOCOH (1.28)	BBMM (1.92)	0.64	33.1	1.53	KDE h-PLUGIN (1.49)	1.02
<b>B -dry</b>	a-LOCOH (0.72)	KDE h-LSCV (1.38)	0.66	47.6	1.02	KDE h-PLUGIN (1.14)	0.62
<b>B -wet</b>	a-LOCOH (0.66)	KDE h-LSCV (2.27)	1.61	71.1	1.34	MCP (1.48)	0.47
<b>A</b>	a-LOCOH (0.15)	KDE h-LSCV (2.54)	2.38	93.9	0.94	MCP (0.94)	0.15
<b>C</b>	k-LOCOH (0.06)	KDE h-LSCV (0.20)	0.15	72.0	0.11	MCP (0.11)	0.08

Table 3

Estimate	Area of overlap (km <sup>2</sup> )	Relative overlap (%)	Percent of yearly home range
<b>MCP</b>	0.85	57.0	53.7
<b>KDE-LSCV</b>	1.20	52.9	64.1
<b>KDE-PLUGIN</b>	0.57	48.2	38.6
<b>k-LoCoH</b>	0.29	34.3	21.7
<b>a-LoCoH</b>	0.17	23.8	13.3
<b>BBMM</b>	1.05	60.9	54.6
<b>Median overlap of seasonal estimates (km<sup>2</sup>)</b>	0.71	50.6	46.1
<b>Estimate closest to median overlap (km<sup>2</sup>)</b>	KDE h-PLUGIN (0.57)	KDE h-PLUGIN (48.2)	KDE h-PLUGIN (38.6)

Table 4

Estimate	MCP	KDE- LSCV	KDE- PLUGIN	k-LoCoH	a-LoCoH
MCP	~	~	~	~	~
KDE- LSCV	74.9% (1.40)	~	~	~	~
KDE- PLUGIN	<b>76.7%</b> <b>(1.21)</b>	<b>78.1%</b> <b>(1.46)</b>	~	~	~
k-LoCoH	<b>84.5%</b> <b>(1.34)</b>	65.8% (1.23)	73.9% (1.10)	~	~
a-LoCoH	<b>81.3%</b> <b>(1.28)</b>	64.7% (1.21)	73.7% (1.10)	<b>95.3%</b> <b>(1.28)</b>	~
BBMM	71.3% (1.37)	<b>79.3%</b> <b>(1.52)</b>	65.5% (1.26)	64.8% (1.24)	62.2% (1.19)



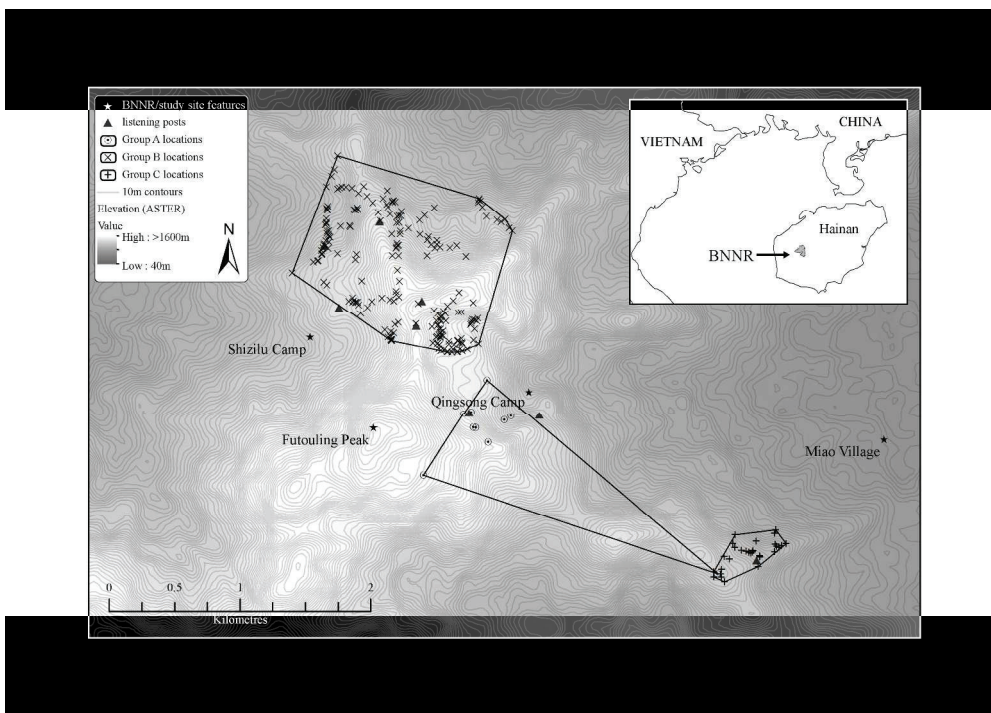


Fig. 1. Location of Hainan gibbon groups in Bawangling National Nature Reserve, showing: ranging location datasets with Minimum Convex Polygons per group, relative locations of groups, and key landscape features. Note the single circular location point for Group A within the cluster of crosses for Group C.

Fig. 1

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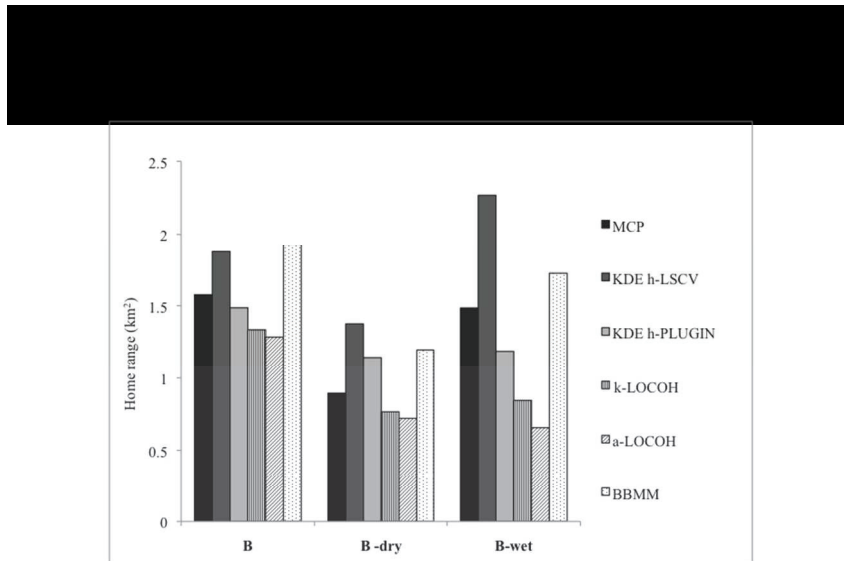


Fig. 2. Group B yearly and seasonal home range estimates (km<sup>2</sup>) by estimation method.  
Fig. 2  
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