

## Effects of protected areas on survival of threatened gibbons in China

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Keywords:	brake effect, gibbon, habitat, nature reserve, population trends, protected area management effectiveness
Abstract:	<p>Establishing protected areas (PAs) is an essential strategy to reduce biodiversity loss. However, many PAs do not provide adequate protection due to poor funding, inadequate staffing and equipment, and ineffective management. As part of China's recent economic growth, the Chinese government has significantly increased investment in nature reserves over the past 20 years, providing a unique opportunity to evaluate whether PAs can protect threatened species effectively. We compiled data on populations of gibbons (Hylobatidae; threatened flagship species with cultural significance) that occurred in Chinese reserves post-1980, and evaluated the ability of these PAs to maintain gibbon habitats and populations. We also assessed the perspective of reserve staff concerning PA management effectiveness. We found that reserves were effective in protecting gibbon habitat by reducing forest loss and human disturbance; however, half of the reserves lost their gibbon populations since being established. Gibbons were more likely to survive in recently established reserves, with higher elevation, less forest loss, less human impact, and more scientific research. A larger initial population size in the 1980s was also positively associated with gibbon persistence. Although all reserves reported increased investment and improved management over the past 20-30 years, no relationship was found between management scores and gibbon population trends. We suggest early investment is critical. This is analogous to preventing a traffic accident: conservation practitioners must brake population decline early, and brake emphatically to prevent extinction.</p>

# 1 **Effects of protected areas on survival of threatened gibbons in China**

2

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23 **Keywords:** brake effect, gibbon, habitat, nature reserve, population trends, protected  
24 area management effectiveness

25

## 26 **Introduction**

27 Many actions have been taken to reduce biodiversity loss, among which the  
28 establishment of protected areas (PAs) is a fundamental global strategy (Margules &  
29 Pressey 2000; Jenkins & Joppa 2009). PAs can be effective in both reducing habitat  
30 loss and stopping declines of threatened wildlife populations (Geldmann et al. 2013).  
31 However, many PAs have not functioned as expected due to various reasons,  
32 including lack of funding, staffing, equipment and training, and ineffective  
33 management (Laurance et al. 2012; Watson et al. 2014). The most extreme examples  
34 are “paper parks”, which are PAs with little or no formal management that do not  
35 provide adequate protection for biodiversity and exist only at the legislative level  
36 (Curran et al. 2004). Therefore, in addition to increasing the number and area of PAs,  
37 promoting their effectiveness is imperative to the success of biodiversity conservation.

38 China is a huge country with a diverse range of habitats that support exceptionally  
39 rich biodiversity, including over 6000 vertebrate species (Xu et al. 1999). However, it  
40 also has the world’s largest human population, and faces a serious biodiversity crisis  
41 following decades of rapid economic growth (Ouyang et al. 2016; Liu et al. 2018). To  
42 reduce biodiversity loss, China has established many nature reserves (the most  
43 common type of PAs in China); as of 2017, 2,750 nature reserves had been  
44 established (Xu et al. 2019). Together with other types of PAs, they cover 20% of  
45 China’s terrestrial area (Ouyang et al. 2018), approximately equivalent to the area of  
46 Peru or 3 times the area of Spain or California. China has also increased financial  
47 investment into its reserves, reaching 5.50 USD/ha in 2009 (Li et al. 2013). However,  
48 the effectiveness of China’s reserves in conserving biodiversity has rarely been  
49 evaluated (Quan et al. 2011; Ren et al. 2015).

50 Among the few species in China for which the effectiveness of conservation actions

51 have been evaluated is the iconic giant panda (*Ailuropoda melanoleuca*) (Kang & Li  
52 2018). Giant pandas receive tremendous conservation investment (currently ~US\$140  
53 million per year for *in situ* conservation), are of high public interest, and are  
54 extremely well researched (Wei et al. 2012; Swaisgood et al. 2018; Li 2020).  
55 However, even the “flagship” reserves for pandas have not protected panda habitat  
56 effectively (Liu et al. 2001; Li et al. 2017). Although recent assessment has shown  
57 that panda populations and habitats have benefited greatly from reserves (Wei et al.  
58 2020), total panda population size and habitat area have not recovered to pre-1988  
59 levels (Wei et al. 2018). This high-profile example raises concerns that conservation  
60 actions for species receiving less attention or investment might be even less effective.

61 Gibbons (Hylobatidae) are small arboreal apes that require intact forest canopy  
62 habitat. They were once widely distributed across China, and were culturally  
63 significant animals in ancient China (Fan 2017; Turvey et al. 2018). Their distribution  
64 has contracted dramatically over the past 400 years due to habitat loss and hunting  
65 (Chatterjee et al. 2012; Turvey et al. 2015; Fan 2017). Populations of 6 gibbon species  
66 survived in fragmented forests in 3 southwestern Chinese provinces (Guangxi, Hainan  
67 and Yunnan) into the 1980s (Fan 2017). To protect these remnant gibbon populations  
68 and their habitats, the Chinese government established a series of reserves, and >80%  
69 of gibbon populations are found within protected areas (Fan 2017). Since 1989 all  
70 gibbons have been listed as Class I protected animals in China. Nonetheless, some  
71 populations continued to decline, and two species were recently extirpated in China  
72 (Grueter et al. 2009; Fan et al. 2014). It is therefore essential to evaluate the  
73 effectiveness of reserves for gibbon conservation in China, and to assess why different  
74 conservation efforts have had such varying levels of success.

75 We compiled data on changes in site-specific population size for all 6 gibbon

76 species that occurred post-1980 in China, and assessed the effectiveness of reserves  
77 on preserving gibbon habitats and populations. We then surveyed staff across reserves  
78 with extirpated or extant gibbon populations, to evaluate if perceived effectiveness of  
79 management explained variation in gibbon population trends. Using gibbons in China  
80 as an example, we aim to evaluate if PAs have been able to reverse population  
81 declines and halt biodiversity loss.

82

### 83 **Methods**

84 We compiled data on the distribution and status of all known recently extant (post-  
85 1980) gibbon populations in China, and on the location, age, and administration level  
86 (national, provincial, and county-level) of all Chinese reserves where gibbons survive  
87 today or have recently occurred, from published literature and first-hand data  
88 collected by our group (Appendix S1). Some reserves consist of discrete management  
89 areas that were founded in different years or are managed by different agencies; these  
90 areas were considered separately. Reserve boundaries were downloaded from the  
91 World Database on Protected Areas (WDPA; <https://protectedplanet.net/>), and were  
92 modified when necessary after consulting reserve staff.

93

#### 94 **Effects of reserves on gibbon habitat**

95 To test whether reserves have been effective at conserving gibbon habitat, we  
96 obtained forest data at 30 m resolution from Global Forest Change 2000–2018  
97 ([https://earthenginepartners.appspot.com/science-2013-global-](https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.5.html)  
98 [forest/download\\_v1.5.html](https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.5.html)), and compared overall forest cover within each reserve to  
99 the surrounding 5 km buffer zone in 2000, as well as percentage forest loss during  
100 2000-2018 as per data availability. We also compared Human Footprint Index (NASA

101 Socioeconomic Data and Applications Center,  
102 <https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-1993-human-footprint>), a  
103 comprehensive index of human pressure on environment at 1 km resolution, for both  
104 1993 and 2009 between reserves and buffer zones. We used non-parametric Mann-  
105 Whitney U tests to conduct comparisons.

106

### 107 **Effects of characteristics of reserves on gibbon populations**

108 We used a logistic regression model to assess the impacts of reserve characteristics on  
109 presence/absence of gibbon populations after 2010 (dependent variable). Uncertain or  
110 unverified reports of local gibbon persistence (e.g., Turvey et al. 2017), were not  
111 accepted as evidence for continued gibbon survival. Reserves or specific management  
112 areas that were established after gibbons had been locally extirpated were excluded.

113 We selected 12 variables based on previous studies that have shown a correlation  
114 with persistence of wildlife populations in PAs (Table 1). We calculated mean  
115 elevation and mean annual temperature of each reserve in ArcGIS version 10.3.1,  
116 based on 90 m resolution DEM data from SRTM v4  
117 (<http://srtm.csi.cgiar.org/SELECTION/inputCoord.asp>) and 30 arc-seconds resolution  
118 temperature data from WorldClim (<http://worldclim.org/version2>). We also calculated  
119 mean topographic ruggedness index (TRI; Riley et al. 1999) derived from the DEM  
120 data. We collected publications about reserves and their gibbon populations by  
121 searching the China National Knowledge Infrastructure (CNKI; <http://www.cnki.net/>)  
122 and Web of Science (<http://apps.webofknowledge.com>). The size of gibbon  
123 populations in the 1980s was obtained from published literature (Appendix S2).

124 All numerical independent variables were tested for collinearity prior to regression  
125 analysis. Elevation and temperature were found to be significantly correlated ( $r = -$

126 0.978,  $p < 0.001$ ), as were forest cover in 2000 and TRI ( $r = -0.761$ ,  $p < 0.001$ ). We  
127 retained elevation and forest cover in 2000 in the set of independent variables.

128 As our sample size was small ( $n = 18$ ), we considered only one variable for each  
129 model and calculated their AICc value. Models with  $\leq 2 \Delta AICc$  were considered as  
130 having an equivalent support to the best model with the smallest AICc value  
131 (Burnham & Anderson 2002). We then calculated Akaike weight ( $\omega_i$ ) for each model.  
132 Since no single model had an  $\omega_i$  over 0.9, we averaged top models that had a  
133 cumulative  $\omega_i > 0.9$  to obtain the coefficient and SE for each variable that was  
134 contained in top models. Relative importance of variables was determined based on  $\omega_i$   
135 of the top models, and variables with SE larger than the absolute value of coefficient  
136 were excluded from the final model. We used the area under the receiver operating  
137 characteristic curve (AUC) to determine performance of the final model, with 1.0  
138 showing perfect discrimination ability and 0.5 showing no discrimination ability  
139 (Pearce & Ferrier 2000).

140

#### 141 **Effects of reserve management effectiveness on gibbon populations**

142 We conducted an online questionnaire survey on reserve management effectiveness  
143 (<https://wj.qq.com/s2/4828422/a27a/>). The questionnaire was based on the  
144 Management Effectiveness Tracking Tool, one of the most widely used systems to  
145 assess management effectiveness of PAs, and on the Technical Regulations for the  
146 Management Effectiveness Evaluation of Nature Reserves (LY/T 1726-2008)  
147 published by the State Forestry Administration of the People's Republic of China. We  
148 included 39 questions in 4 groupings (following Geldmann et al. 2017), including: A–  
149 Design and Planning (9 questions), B–Monitoring and Enforcement (11 questions),  
150 C–Capacity and Resources (9 questions), and D–Decision-making Arrangement (10

151 questions). We contacted reserve staff and asked them to recall information from the  
152 1980s, 1990s, 2000s, and 2010s, and then to fill out the questionnaire by self-scoring  
153 the performance of their reserves during each decade. Scores are integers and  
154 represent reserve performance from worst (0) to best (3); we provided a criterion for  
155 each score alongside the questions.

156 We aimed to find 3 participants from each reserve and recorded the year when they  
157 were employed. For each participant we summed the scores of all 39 questions, and  
158 the scores of questions included within each of the 4 groupings during each decade.  
159 We only included scores from participants for the decades during which they worked  
160 at their reserve. We calculated mean scores across all participants from the same area,  
161 and used these values as indices of management effectiveness. We used a Friedman  
162 rank sum test with a post-hoc Conover test to compare these scores across different  
163 decades to determine change in reserve management effectiveness over time. Since  
164 only 5 areas had staff who had worked there since the 1980s, data from these 5 sites  
165 only were used to compare scores from the 1980s onwards. Data for more reserves or  
166 management areas were available from the 1990s onwards, so we conducted an  
167 additional comparison for this time series.

168 We then assessed the relationship between change of management effectiveness  
169 scores and gibbon population trends. Population trends were determined by  
170 comparing available estimates of gibbon populations between contiguous decades  
171 (based on data listed in Appendix S1), and classified as decreasing (estimates in the  
172 latter decade were smaller than those in the former decade, without range overlap),  
173 stable (estimates with range overlap), and increasing (estimates in the latter decade  
174 were larger and without range overlap). Since there were very few population trends  
175 classified as stable or increasing, we combined these two categories as non-



176 decreasing. We then calculated change of management scores, as well as percentage  
177 change between those contiguous decades in which gibbon population trends were  
178 determined. We used a Mann-Whitney U test to compare mean scores for all  
179 questions and for questions in the 4 groupings between decreasing and non-decreasing  
180 events.

181 All analyses were conducted in R v3.5.0 (R Core Team 2016), using the packages  
182 ggplot2 (Wickham 2016), MuMIn (Bartoń 2016), usdm (Naimi et al. 2014), PMCMR  
183 (Pohlert 2014), raster (Hijmans 2020), and ROCR (Sing et al. 2005).

184

## 185 **Results**

### 186 **Change in gibbon survival and population size in reserves**

187 Gibbon populations recently occurred in areas covered today by 24 Chinese reserves  
188 or 32 distinct reserve management areas (Appendix S1). Huanglianshan used to  
189 contain both northern white-cheeked gibbon (*Nomascus leucogenys*) and western  
190 black crested gibbon (*N. concolor*) but both species are now extirpated, and Nangunhe  
191 used to contain both lar gibbon (*Hylobates lar*) and *N. concolor* in separate areas but  
192 now only contains ~ 2 groups of *N. concolor*. Other reserves or management areas  
193 only have, or used to have, one gibbon species.

194 Most reserves or management areas (63%) were established in the 1980s, with 7  
195 established after gibbons had been locally extirpated in previous decades. The status  
196 of gibbon populations could not be determined at the time of establishment of 4  
197 reserves or management areas. Gibbons disappeared in 10 areas after their  
198 establishment, and only 11 retained gibbons into the 2010s.

199 Among the 32 management areas, 21 had been upgraded since their establishment,  
200 with 20 of them upgraded from provincial-level to national-level, and one from

201 county-level to provincial-level (Appendix S1). Upgrades occurred 13.7 (SE 1.7,  
202 range: 3–28) years after reserves were founded, in the year 1999 (SE 2, range: 1986–  
203 2014). Among the 10 areas where gibbons disappeared after reserve establishment, 6  
204 had been upgraded. However, gibbons disappeared in 4 areas before reserves were  
205 upgraded. Eight out of 11 areas where gibbons survived into the 2010s had been  
206 upgraded, and the percentage of reserves having been upgraded in this group was not  
207 different from that in the group of reserves where gibbons disappeared ( $\chi^2 = 0.077$ , df  
208 = 1,  $p = 0.782$ ).

209

### 210 **Effects of reserves on gibbon habitat**

211 Forest cover in 2000 was higher within reserves than in the buffer zones surrounding  
212 each reserve (72.3, SE 2.2 vs. 52.6, SE 2.6,  $W = 867$ ,  $p < 0.001$ ; Fig. 1a), and  
213 percentage forest loss was higher in buffer zones than within reserves (2.63, SE 0.78  
214 vs. 8.11, SE 0.97,  $W = 128$ ,  $p < 0.001$ ; Fig. 1b). We found no difference in Human  
215 Footprint Index between reserves and buffer zones in 1993 (7.95, SE 0.36 vs. 8.48, SE  
216 0.31,  $W = 423$ ,  $p = 0.234$ ; Fig. 1c), but there was a significant difference in 2009 ( $p <$   
217  $0.001$ ; Fig. 1d), with less human impact within reserves (7.74, SE 0.23) than in buffer  
218 zones (9.05, SE 0.26).

219

### 220 **Effects of reserve characteristics on gibbon populations**

221 Six of the 10 independent variables were retained in the final model, having  
222 significant impacts on gibbon survival into the 2010s (Table 2, 3). The AUC for the  
223 final model was 0.975, indicating good discriminatory ability. In general, gibbons  
224 were more likely to survive in more recently established reserves, and in reserves

225 located at higher elevations. Percentage forest loss and percentage Human Footprint  
226 Index change were negatively correlated with gibbon survival, and number of papers  
227 published was positively correlated with gibbon survival. Gibbon populations with a  
228 larger initial size in the 1980s were also more likely to survive into the 2010s. Forest  
229 cover and reserve administration level (either current or at foundation), and whether  
230 reserve had been upgraded, were not correlated with gibbon survival.

231

### 232 **Effects of reserve management effectiveness on gibbon populations**

233 Sixty people from 21 reserves or management areas participated in our questionnaire  
234 survey. Excluding records without clear reserve or management area identification,  
235 we retained 49 records from 19 areas, with a mean of 2.6 participants per area (range:  
236 1–6). Participants had worked in their reserves for a mean of 14.7 (SE 1.5) years.

237 Management effectiveness scores increased over time (all  $p \leq 0.003$ ), both from the  
238 1980s (for 5 areas; Fig. 2a, Appendix S3) and from the 1990s (for 13 areas; Fig. 2b,  
239 Appendix S3). No changes of score or percentage changes between contiguous  
240 decades (either of all questions or of question groupings) were found to be different  
241 between decreasing ( $n = 8$ ) and non-decreasing ( $n = 4$ ) gibbon populations in  
242 corresponding decades (all  $p > 0.05$ , Appendix S4). This result indicates there was no  
243 significant relationship between trends of gibbon populations and change/percentage  
244 change of management scores (of all questions or of question groupings).

245

## 246 **Discussion**

247 We evaluated the conservation effectiveness of Chinese PAs at protecting threatened  
248 gibbon populations and habitat. Over 80% of China's gibbons now live inside  
249 reserves (Fan 2017), but while we found that reserves were effective in protecting

250 gibbon habitat through reducing forest loss and human impacts, they did not function  
251 well at protecting gibbon populations. Almost half of the reserves in China that  
252 formerly contained gibbons have lost these populations in the few decades since they  
253 were established, and gibbons have never recolonized a reserve in China once they  
254 became locally extirpated.

255

### 256 **Effectiveness of reserves for conserving gibbon habitat and populations**

257 Our analyses demonstrate that forest cover inside gibbon reserves is higher than in the  
258 surrounding buffer zones, and forest loss and human impacts are lower inside these  
259 reserves. This result indicates that reserves have been effective at protecting habitat  
260 compared to the status of their wider landscapes (cf. Geldmann et al. 2013). Some  
261 regional case studies have demonstrated that PAs are not always effective at  
262 maintaining habitat (Brower et al. 2002; Curran et al. 2004), and further steps are  
263 required to fulfill their conservation potential (Watson et al. 2014). However, many  
264 PAs are effective in reducing forest loss and anthropogenic activities inside their  
265 boundaries, including other PAs in China (Wei et al. 2020).

266 However, whereas these reserves have generally protected gibbon habitat, they  
267 were not effective at protecting gibbon populations. Gibbons disappeared in almost  
268 half of the reserves or management areas since they were established. We identified  
269 several reserve characteristics that affected gibbon survival (Table 3). Initial  
270 population size of gibbons in the 1980s was positively associated with gibbon survival  
271 into the 2010s. This result is in accordance with the common pattern that small  
272 populations are more likely to become extinct due to inbreeding, genetic drift and  
273 demographic stochasticity, as well as increased vulnerability to hunting or other  
274 anthropogenic disturbance (e.g., Saccheri et al. 1998; Legendre et al. 1999). However,

275 the Hainan gibbon (*N. hainanus*) population at Bawangling is an exception to this  
276 general pattern. This population decreased to 7-9 known individuals in 1989 (Liu et  
277 al. 1989) and contained only 13 known individuals in 2003 (Zhou et al. 2005), but has  
278 now increased to more than 30 individuals (Chan et al. 2020). Nevertheless, the  
279 relative importance of initial population size was low (Table 3), suggesting that other  
280 variables have been more influential in determining gibbon survival in Chinese  
281 reserves.

282 Although forest loss in reserves was lower than in their surrounding buffer zones,  
283 loss still occurred inside reserves (see also Zhang et al. 2010), and percentage forest  
284 loss was inversely correlated with gibbon survival. Furthermore, our study assessed  
285 overall forest cover but not forest quality. Gibbons rely heavily on mature,  
286 undisturbed evergreen forest (Phoonjampa et al. 2011), and specific anthropogenic  
287 activities such as cardamom planting reduce the quality of gibbon habitat (Yuan et al.  
288 2014). Such changes in habitat quality may explain why we found no correlation  
289 between forest cover and gibbon survival, and further investigation of both quantity  
290 and quality of gibbon habitat is needed.

291 We found that gibbons were more likely to survive in reserves at higher elevations  
292 (and with lower temperatures). This finding is consistent with longer-term patterns of  
293 local survival or extinction of gibbon populations across China during recent centuries  
294 (Chatterjee et al. 2012; Turvey et al. 2015). These patterns likely reflect the fact that  
295 lower-elevation landscapes typically have higher human populations and more  
296 associated anthropogenic pressures including poaching, agricultural encroachment,  
297 and livestock grazing (Fan & Jiang 2010). Indeed, this likelihood is supported by our  
298 additional result that increased Human Footprint Index within reserves, a measure of  
299 the negative impacts associated with anthropogenic activities, was negatively

300 associated with gibbon survival.

301 The number of papers published on gibbons and their reserves was positively  
302 correlated with gibbon presence. It is possible that researchers have conducted more  
303 studies in areas where gibbon populations are healthy and well managed.  
304 Alternatively, scientific research has been demonstrated to help wildlife conservation  
305 through raising public awareness and concerns about threatened species, improving  
306 management of reserves through science-based decision-making, and attracting  
307 additional funding (Pusey et al. 2007; Hu et al. 2019). More importantly, gibbon  
308 studies, especially behavioral ones, usually require long-term fieldwork, and the  
309 presence of researchers and research sites in forests may be one of the most effective  
310 ways to prevent poaching (Piel et al. 2015; Chapman et al. 2017). We therefore  
311 encourage more long-term field studies, not only to improve our understanding of the  
312 conservation status and requirements of threatened populations, but also to support  
313 their practical protection.

314 We found that age of reserve was negatively associated with gibbon survival,  
315 contrary to our prediction that the earlier a landscape received protection, the greater  
316 the likelihood that populations would persist (Friedlander et al. 2017). This result  
317 clearly demonstrates that establishment of a reserve does not mean that its gibbons  
318 immediately received effective protection. Reserves founded several decades ago may  
319 not have received sufficient investment, and management effectiveness may have  
320 initially been low (Han 2000; Li et al. 2013). Our results also showed that human  
321 impacts within reserves did not differ from surrounding buffer zones in 1993, but  
322 were lower than in buffer zones in 2009, indicating low management effectiveness in  
323 earlier stages but improved effectiveness later on. In addition, other factors such as  
324 traditional ecological knowledge and strict local regulation on guns may also have

325 contributed to survival of gibbon populations in some unprotected landscapes before  
326 reserves were established, and continued to influence local gibbon survival after  
327 reserve establishment (Ma et al. 2019; Zhang et al. 2020).

328 We found no relationship between reserve administration level (current-day level,  
329 level at foundation, and whether reserve had been upgraded) and gibbon survival. A  
330 higher level of administration usually means more investment and probably more  
331 effective management (Quan et al. 2011). However, our findings suggest that  
332 administration level does not reflect management effectiveness for specific gibbon  
333 populations. Gibbons have a low reproductive rate, with females breeding every 3-5  
334 years, and are thus very sensitive to poaching (Fan & Jiang 2007; Phoonjampa &  
335 Brockelman 2008). Although poaching is strictly prohibited across Chinese reserves,  
336 it does occur in many reserves in China, including national-level reserves (Gong et al.  
337 2017). For sensitive gibbon populations, any management improvement brought by  
338 upgraded administration level can be counteracted by a single poaching event.

339

#### 340 **The importance of early investment in reserves for species conservation**

341 Two-thirds of reserves or management areas had been upgraded, with most of them  
342 upgraded from provincial-level to national-level, and no area had been downgraded.  
343 On average, reserves were upgraded 14 years after establishment, and with most  
344 upgrading occurring around 1999. Our findings are in accordance with other studies  
345 showing that China has dramatically increased investment in reserves since 2000 (Li  
346 et al. 2013). Similarly, reserve staff who participated in our questionnaire survey all  
347 reported management effectiveness scores that increased over time (Fig. 2).  
348 Comparisons of Human Footprint Index between reserves and surrounding buffer  
349 zones also indicate an increased general management effectiveness of reserves, a

350 pattern also seen in many other PAs around the world (Geldmann et al. 2015).

351       Nonetheless, this increase in management scores was not associated with positive  
352 gibbon population trends over time. This is concerning, as it suggests that increased  
353 investment in existing reserves does not automatically increase survival prospects for  
354 gibbons. This lack of correlation may be because many reserves were established at a  
355 point when gibbon populations were rapidly declining or already on the edge of  
356 extinction. However, our results also suggest that reserves established longer ago  
357 suffered from limited investment and low management effectiveness. If effective  
358 investment during this crucial early time window was missed, subsequent increases in  
359 investment appeared to be unable to preserve gibbon populations.

360

### 361 **Conservation implications**

362 We demonstrate that establishment of PAs has not ensured gibbon survival in China.  
363 Although it is not possible to determine the critical time window when there was a  
364 “best last chance” to save each of these now-extirpated gibbon populations, we argue  
365 that immediate investment at early stages (i.e., when PAs were established) is likely to  
366 be most helpful for the conservation of such small threatened populations. This is  
367 analogous to preventing a traffic accident: conservation practitioners must brake  
368 population decline at an early stage, and brake emphatically, to have the best chance  
369 of preventing extinction. Nevertheless, delayed investment is better than no  
370 investment; conservation efforts have saved many vertebrate species from extinction  
371 worldwide (Hoffmann et al. 2010), and even tiny remnant populations can recover,  
372 even if they have persisted at very low sizes for several decades (Crees et al. 2016).  
373 Indeed, such potential for conservation recovery is shown within our study by the  
374 Hainan gibbon, which—although still extremely rare and vulnerable—is showing



375 encouraging signs of population recovery (Bryant et al. 2016; Chan et al. 2020).  
376 “Although time is running out, there is still an enormous amount of nature left to fight  
377 for” (Balmford 2012).

378

### 379 **Supporting Information**

380 Basic information about reserves (Appendix S1), detailed methods for calculating  
381 gibbon population size in the 1980s (Appendix S2), comparison of management  
382 effectiveness scores between decades (Appendix S3), and trends of gibbon  
383 populations and changes of management scores (Appendix S4), are available online.  
384 The authors are solely responsible for the content and functionality of these materials.  
385 Queries (other than absence of the material) should be directed to the corresponding  
386 author.

387

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- 572



573 **Tables**

574 Table 1. Independent variables included in logistic regression models investigating characteristics of nature reserves that were associated with  
 575 gibbon persistence into the 2010s.

Variable	Description	Prediction	Reference	Data source / resolution
LEV*	Administration level: a) national; b) provincial; c) county-level	Higher-level reserves have stricter regulations, so provide greater protection to gibbon populations	(Dudley 2008)	Reserve websites / NA
AGE	Age of reserve (years)	Reserve age is positively correlated with gibbon population survival	(Claudet et al. 2008; Phoonjampa et al. 2011)	Reserve websites / NA
ELE	Mean elevation of reserve (m)	Higher elevation has negative impact on gibbon populations due to food limitation	(Fan & Jiang 2010)	SRTM v4 / 90 m

TRI	Mean topographic ruggedness index within reserve	More rugged terrain is beneficial to gibbon survival	(Li et al. 2014; O'Neil et al. 2020)	Calculated from SRTM DEM v4 / 90 m
TEM	Mean annual temperature (°C)	Lower temperature has negative impact on gibbon populations	(Fan et al. 2013)	WorldClim / 30 arc-seconds
FOR	Forest cover in year 2000	Higher forest cover provides better habitat for gibbons	(Phoonjampa et al. 2011)	Global Forest Change 2000–2018 / 30m
PFL	Percentage forest loss during 2000-2018	Forest loss has negative impact on gibbon populations	(Phoonjampa et al. 2011)	Global Forest Change 2000–2018 / 30 m
HFI	Percentage HFI change during 1993-2009	Human disturbance has negative impact on gibbon populations	(Fan & Jiang 2010)	NASA Socioeconomic Data and Applications Center / 1km
PAP	Number of papers published in both Chinese and English referring to reserve and its gibbon population	Scientific research benefits threatened species conservation	(Hu et al. 2019)	China National Knowledge Infrastructure, Web of Science / NA
POP	Size of gibbon populations in	Small populations are more likely to	(Saccheri et al. 1998)	Published literature and first-

the 1980s

become extinct

hand data

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576 \*Including 3 variables: current administration level, level at reserve establishment, and whether reserve had been upgraded.

577

For review only

578 Table 2. Logistic regression models, ranked by their AICc, explaining  
 579 presence/absence of gibbons in 18 reserves or management areas after 2010 based on  
 580 10 independent variables. Loglik, log-likelihood;  $\Delta$ AICc, difference in AICc values  
 581 between each model and the best model;  $\omega_i$ , Akaike weight.

Variables	LogLik	AICc	$\Delta$ AIC	$\omega_i$
Elevation	-9.37	23.535	0.000	0.228
Reserve age	-9.38	23.555	0.019	0.226
Papers	-9.45	23.707	0.171	0.210
Percentage forest loss	-9.93	24.660	1.125	0.130
Gibbon population size in 1980s	-10.32	25.448	1.913	0.088
Percentage HFI change	-10.71	26.213	2.678	0.060
Forest cover in 2000	-10.98	26.750	3.215	0.046
Administration level at founded	-11.75	28.308	4.773	0.020
Whether reserve had been upgraded	-12.14	29.074	5.538	0.014
Current-day administration level	-12.34	29.475	5.940	0.011

582

583 Table 3. Model-averaged coefficients and relative importance of variables for logistic  
 584 regression models analyzing variables associated with presence/absence of gibbons in  
 585 18 reserves or management areas after 2010.

Variables	Coefficien t	SE	Relative importance based on $\omega_i$
(Intercept)	0.312	2.881	
Elevation	0.002	0.001	0.242

Reserve age	-0.113	0.062	0.240
Papers	0.370	0.304	0.223
Percentage forest loss	-0.941	0.588	0.138
Gibbon population size in 1980s	0.018	0.012	0.093
Percentage HFI change	-9.968	6.111	0.064

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586

587

588 **Figures**

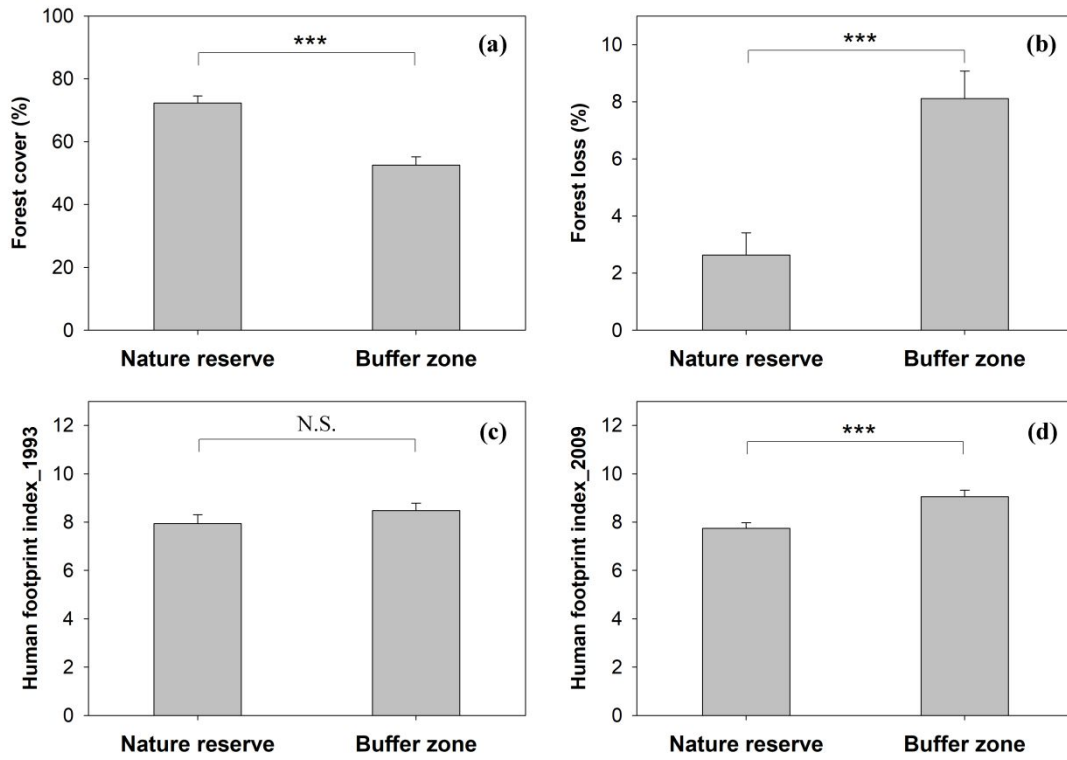
589 Figure 1. Comparison of forest cover in 2000, percentage forest loss in 2000–2018,  
 590 and human footprint indices in 1993 and 2009, between reserves and their 5 km buffer  
 591 zones. \*\*\*difference significant at  $P < 0.001$ . N.S. difference not significant.

592

593 Figure 2. Comparison of mean scores of all questions (All) and of 4 question  
 594 groupings (G1: Design and Planning, G2: Monitoring and Enforcement, G3: Capacity  
 595 and Resources, G4: Decision-making Arrangement) across decades. Different  
 596 lowercase letters indicate significant differences at  $P < 0.05$ .

597

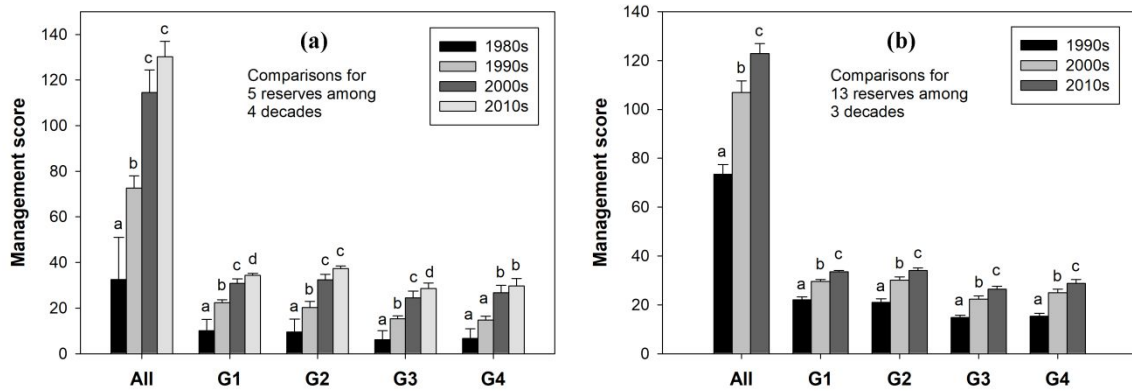
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599

600 Figure 1.

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602

603 Figure 2.

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