Developing a conservation evidence-base for the Critically Endangered Hainan gibbon (*Nomascus hainanus*)

Jessica V. Bryant

Division of Biosciences, University College London (UCL)
Institute of Zoology, Zoological Society of London

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Declaration

I, Jessica Victoria Bryant, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated and appropriately referenced within the thesis.

Abstract

The Critically Endangered Hainan gibbon (*Nomascus hainanus*) is the world's rarest ape, with a single population of an estimated 25 individuals surviving in approximately 15 km^2 of suboptimal forest within Bawangling National Nature Reserve, Hainan, China. The existing biological evidence-base for the species is inadequate for conservation planning, precluding evaluation of appropriate recovery actions. I derived comprehensive new baseline data on Hainan gibbon ecology, behaviour and genetics to clarify the species' biology and population status, and inform urgently required conservation management for the species. Rigorous re-evaluation of Hainan gibbon spatial requirements indicated the species' home range is much smaller than previously estimated (c. 1.5 km^2) and in line with closely related *Nomascus* species in similar ecological conditions. Molecular assessment of the genetic status of the surviving population within the context of the species' historical genetic diversity revealed that the Hainan gibbon has suffered a significant decline in genetic diversity following its past population bottleneck. The current population also shows a high level of relatedness and male-biased offspring sex ratio. Predictive models examining reportedly 'anomalous' Hainan gibbon ecological and behavioural traits within a phylogenetic framework indicated that large, polygynous groups may be evolutionarily characteristic for the species, but home range requirements are influenced by both intrinsic factors and current extrinsic conditions. Finally, Population Viability Analysis demonstrated that the species is highly likely to become extinct in the near future without active management, and that multiple actions mitigating extrinsic threats, enhancing habitat carrying capacity and improving survivorship will be required to reduce extinction risk. Together, these findings suggest that landscape-level management actions and intensive manipulation of the population may be necessary to safeguard the future of the Hainan gibbon. This research also has wider implications for improved understanding of gibbon ecology and conservation of species of extreme rarity.

Chinese Summary

构建极度濒危物种海南长臂猿 (*Nomascus hainanus*) 的保护学依据

杰西卡 布莱恩特

英国伦敦大学学院, 生命科学系
伦敦动物学会，动物研究所

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摘要

极度濒危的海南长臂猿 (*Nomascus hainanus*) 是全球最为珍稀的类人猿，它们仅存一个由25 个个体组成的种群，栖息在中国海南岛霸王岭国家级自然保护区内约 15 km^2 的次优林中。由于现有的关于该物种的生物学研究不足，理论依据的匮乏进一步限制了制定及评估其适宜的种群恢复行动。本研究为海南长臂猿的保护构建了一个综合的、全新的基础数据库，包括反映其生物学及种群现状的生态学、行为学和遗传学方面的数据，同时提出了该物种亟需的保护管理要求。本研究对海南长臂猿的空间需求进行了一次严谨的二次评估，结果显示该物种的活动范围比之前估计的 (1.5 km^2) 要小得多，与在相同生态条件下的、与其十分相近的黑冠长臂猿属一致。另外，针对现存种群进行的种群遗传学分子评估发现，受到过去种群数量的瓶颈限制，海南长臂猿的遗传多样性与其历史相比经历了严重的下降。现有的群体表现出了高度的亲缘性及后代的雄性性别偏向性。预测模型在系统发生学的框架下进一步分析了海南长臂猿的“反常”生态及行为特征，揭示了大的、一夫多妻的种群可能是该物种的进化特点，而其对活动范围的需求则同时受到内在因素和当前外在条件的影响。最后，种群生存力分析演示了该物种可能面临的灭绝风险，若不采取积极的、多元化的保护管理以缓解外界威胁、提高栖息地承载力及增加存活率，该物种很可能在不远的将来面临灭绝。总而言之，本研究的发现认为采取景观层面的宏观管理行动及实施强力的种群保护操作是保证海南长臂猿长远生存的必要手段。同时，本研究促进了对长臂猿生态学及针对极度稀少物种保护方面的了解，具有更为广泛的影响及参考意义。

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When first contemplating this project I knew I was in for a challenge, that was the lure, but I had little idea it would take me on quite such an epic journey both professionally and personally. I am sincerely grateful to my supervisors, Sam Turvey, Helen Chatterjee, John Fellowes and Guy Cowlishaw, for giving me the opportunity to embark upon this adventure, and for the continual support and guidance throughout. Applied postgraduate research projects at the very coalface of conversation don't come along very often, and I count myself as extremely fortunate to have been permitted to study and hopefully actively contribute to the conservation of this remarkable animal.

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-van Gulik, 1967

朝辞白帝彩云间
千里江陵一日还
两岸猿声啼不住
轻舟已过万重山

李白

White King City I left at dawn in the morning-glow of the clouds,
The thousand miles to Chiang-ling we sailed in a single day.
On either shore the gibbons' song sounded without pause,
While my light boat skimmed past ten thousand sombre crags.

-Lǐ Bái, c.756 A.D.

Chapter 1. General Introduction

Conserving species of extreme rarity

Our planet is in the midst of an extinction crisis. Species losses are occurring at an unprecedented rate, between 100 and 10,000 times higher than pre-human rates characterised in the fossil record (Pimm et al. 1995, Mace et al. 2005). This global extinction crisis, dubbed “the sixth extinction” (Barnosky et al. 2011), is the most recent wave of mass extinction in the history of life on Earth, but is the first to have been triggered by human actions (Leakey and Lewin 1996). Intense and increasing human pressures, including resource exploitation (of species and their habitats), habitat loss and fragmentation, invasive species introductions, spread of pathogens, and global climate change, are individually and synergistically driving biodiversity loss (Brook et al. 2008, Laurance and Useche 2009). The IUCN Red List, the most comprehensive global assessment of extinction risk, reports that an estimated 25% of mammal species, 13% of bird species, and 41% of amphibian species are now threatened with extinction (IUCN 2013). These figures are set to increase; the population of one in two mammal species is declining (Schipper et al. 2008), and, on average, more than fifty species of mammals, birds, and amphibians move one Red List category closer to extinction each year (Hoffmann et al. 2010). Consequently, an increasing number of species are on the brink of extinction, and the prevalence of species of extreme rarity, those species that are not only Critically Endangered (the highest Red List category) but reduced to only a handful of individuals, is rising.

This current extinction crisis is generating an escalating conservation crisis, and conservation management decisions must be made rapidly to prevent further species losses. Early conservation ideas (Soulé and Wilcox 1980, Soulé 1985, Soulé 1987) concentrated on the population consequences of scarcity or ‘smallness’ that affect species at risk of extinction; the ‘small-population paradigm’. Caughley (1994) argued that the management generalities suggested by the largely theory-driven small-population paradigm are alone unlikely to be sufficient, and that an integration of this and the ‘declining-population paradigm’, concerned with detecting, diagnosing and halting a population decline through a focus on empirical data and case-by-case assessment, is vital to successful conservation. In recent years, the importance of evidence-based conservation has become apparent. This approach involves the systematic collection and evaluation of robust, objective, empirical data on a threatened species’ ecology, population dynamics and threats to guide management decisions (Pullin and Knight 2001, Sutherland et al. 2004, Stewart et al. 2005, Segan et al. 2011). Unfortunately, for exceptionally rare species, which constitute those species of highest conservation concern, their very rarity makes them inherently difficult to study. So, paradoxically, for species on the edge of extinction, and most urgently in need of management action, robust data are often unavailable.

This can lead to delays in conservation action, as appropriate actions cannot be identified, which in turn risks further decline and extinction (Rabinowitz 1995, Groombridge et al. 2004, Turvey 2008, Grantham et al. 2009).

So how do we make decisions about appropriate conservation actions for species of extreme rarity, where action could prove the difference between extinction and recovery? To gather sufficient information to inform an evidence-based conservation approach for such species, it is necessary to utilise a wide scope of methods. It is increasingly recognised that a multifaceted approach, employing genetic, demographic, ecological, and population and ecological modelling data, is required for effective conservation planning (Crandall 2009, Gebremedhin et al. 2009). A number of quantitative tools are now available to aid conservation planning, including population viability analysis (PVA) (Akçakaya and Sjogren-Gulve 2000), risk assessment (Burgman et al. 1993), decision analysis (e.g. Drechsler 2000, Maguire 2006, VanderWerf et al. 2006), and operational models (e.g. investigating action implementation possibilities; Knight et al. 2006). Furthermore, it is clear that conservation managers employ a complex array of information when making management decisions, including data pertaining to species' ecology and threats to species, and evidence that will assist prioritisation of management actions (Cook et al. 2012). Therefore, for Critically Endangered species, where numbers are precariously low and the stakes are high, it is imperative that every available tool be used to consider individual potential management issues and evidence for (or against) possible management strategies, in order to inform conservation planning and identify appropriate recovery actions.

The mammal conservation crisis in China

While globally, one in four mammal species is threatened with extinction, the highest concentration of threatened land mammals is found in the regions of South and Southeast Asia (Schipper et al. 2008). In addition to an outright decline in the number of species, the ranges of many surviving large mammals have substantially contracted in Asia in the recent historical period (since A.D. 1500) (Morrison et al. 2007). In China, nearly 960 species (483 animals, and 475 plants) are presently listed as Critically Endangered, Endangered or Vulnerable (IUCN 2013), making it one of ten countries with the highest numbers (>900) of species at risk of extinction (not controlling for land mass, survey effort, or intrinsic biodiversity). Mammals account for 75 of these species, and of those approximately 13% are Critically Endangered, and so face an extremely high probability of extinction. In fact, this is likely to be a conservative representation of the situation, with a further 54 mammal species (of 913 animal species) in China being Data Deficient, preventing formal assessment for Red List categorisation (IUCN 2013), and many other species are likely to already be lost.

China has some undesirable distinctions in its record of mammal extinction. The loss of the Yangtze river dolphin or baiji (*Lipotes vexillifer*), an endemic Chinese mammal, signified the first documented global extinction of a megafaunal vertebrate in over 50 years (Turvey et al. 2007). Another Chinese endemic, and one of only two mammals across the globe officially regarded as 'Extinct in the Wild', Père David's deer (*Elaphurus davidianus*), now persists only in captivity (Jiang and Harris 2008). Several other mammal species are also now regionally extinct from China. For example, the Mongolian saiga (*Saiga tatarica*) was reportedly extirpated by the 1960s (Mallon 2008), and two species of gibbon (*Hylobates lar*, *Nomascus leucogenys*) have apparently now also been lost from the Chinese mammalian fauna assemblage (Fan and Huo 2009, Grueter et al. 2009a, Fan et al. 2013a). Other species are declining rapidly, for example the Yangtze finless porpoise (*Neophocaena asiaeorientalis*; Zhao et al. 2008, Mei et al. 2012), and the Chinese pangolin (*Manis pentadactyla*; Duckworth et al. 2008).

Fundamental to this pattern of extinction and decline are specific aspects of China's cultural legacy which have produced historical and ongoing patterns of anthropogenic alteration and over-exploitation of the environment. The threats of habitat loss and degradation, along with direct harvest of fauna and flora are global problems, constituting the main threats to mammals worldwide (Schipper et al. 2008). In China, however, one of the world's most ancient civilisations, the natural environment has seen several thousand years of human alteration (Turvey et al. 2013). This impact was at its most extreme in the 20th century during the communist era, notably including the period of the Great Leap Forward (1958-1961), under Mao Zedong's political rein. Declaring "Man Must Conquer Nature", Mao's 'war against nature' had a devastating impact upon China's environment. In an urgent quest to industrialise and modernise the nation into a utopian socialist society, there was rapid, widespread deforestation, dam construction, and the introduction of extreme agricultural practices, that together saw the landscape altered and impoverished in an attempt to tame nature and increase productivity (Shapiro 2001). Although the Great Leap Forward ended with the Great Chinese Famine in 1961, 'progress' has continued, and the impact on the environment has intensified in the 21st century with an unmatched level of economic growth. Since 1979, the Chinese economy has roughly doubled every eight years, and by 2011 China had the world's second biggest GDP (WorldBank 2013a). China's economic growth appears to be relentless, with an annual GDP growth rate over five times that of the United States of America and almost 12 times that of the United Kingdom (WorldBank 2013b). China's population has also shown record levels of growth as a result of Mao's legacy of pro-nationalism (a belief that as human labour can overcome any obstacle, the more people the better), and now, as the world's most populous nation, China's vast economic wealth and sheer number of people are fuelling natural resource depletion as unsustainable as that carried out by the West for centuries, but at a higher level and greater speed (Harris 2007).

In addition to this general conversion of habitats and extraction of natural resources, China has a long history of active exploitation of animal products which is further escalating its environmental impact (Simons 2013). Wildlife harvesting for Traditional Chinese Medicine has long been acknowledged as a significant driver of biodiversity loss and a conservation challenge which is difficult to address, with Shen et al. (1982 p. 344) remarking: “The single most important factor hampering wildlife conservation in China is the traditional use of wild animals for medicinal purposes, meat and skins”. This points to an underlying philosophy towards nature, and animals in particular, as a ‘resource’, which was further entrenched during the Mao era. Additional social changes during that period, which reached a head during the Cultural Revolution (1966-1976), led to substantial upheaval in traditional attitudes towards the environment (Shapiro 2001). This combination of cultural factors has produced an escalating pressure on environmental resources and conflict with wildlife that has culminated in a conservation crisis in China that shows no signs of waning.

Conservation has been developing in China since the 1980s, when a collaborative giant panda (*Ailuropoda melanoleuca*) conservation programme was established, but there have been ongoing issues with international involvement (Schaller 1993, Turvey 2008). This has, in part, been due to inevitable socio-political considerations, but also an apparent fundamental difference between Western and Chinese approaches to what constitutes ‘conservation’. Western conservation strategies generally try to include an *ex situ* breeding strategy as a last resort for management, or as part of a recovery strategy in combination with *in situ* actions addressing various factors requiring mitigation (e.g. threatening processes). In China, however, there has been a tendency to regard *ex situ* captive breeding as all that is required, with conflicts between Chinese and international researchers on this issue plaguing both the early days of panda conservation (Schaller 1993) and efforts to develop a recovery programme for the baiji (Turvey 2008). This difference in approach is the result of a cultural difference in the appreciation of animals, underpinned by the Chinese prioritisation of the pragmatic and utilitarian value of wildlife above all other values (Harris 2007). The commodification of animals of conservation significance is most poignantly illustrated by the use of pandas as a ‘soft-power’ resource, with strategic ‘*guānxì* trade loans’ being used to influence bilateral negotiations between China and prospective international trading partners (Buckingham et al. 2013). As a result, *in situ* conservation of Chinese species can be a particular challenge, and enhancing our understanding of *in situ* populations is especially important. The situation in China presents one of the greatest global challenges to the conservation community.

The status of gibbons in China

Gibbons (Family Hylobatidae) are distributed throughout the tropical and subtropical rainforests of Southeast Asia, from the Greater Sunda Islands of Java, Sumatra and Borneo to the north-eastern states of India (Figure 1.1). Globally, the Hylobatidae are the most threatened primate family. Of the 19 currently recognised gibbon species (Chivers et al. 2013), four are listed as Critically Endangered by the IUCN, 13 as Endangered, one is listed as Vulnerable, and a further species is yet to be evaluated (IUCN 2013). This last species represents the most recently designated crested gibbon, *Nomascus annamensis*, which suffers a reduced distribution and similar threats to those of other gibbons (Rawson et al. 2011), and so is also likely to be threatened. Not one gibbon species has a population that can be confidently regarded as stable or increasing, and an alarming number of gibbon populations and species are on the brink of extinction (Rawson et al. 2011, IUCN 2013).

Literary and fossil records indicate that gibbons were once widely distributed across China. Based on gibbon fossils and archaeological records from the Pleistocene-Holocene (Gao et al. 1981, Chatterjee et al. 2012), inscriptions from the Shang Dynasty (1500-1200 B.C.) (van Gulik 1967), and gazetteer records from the later Chinese historical record (Wen 2009), the historical distribution of what were most likely crested gibbons (genus *Nomascus*) stretched across southern and central China, up to the Three Gorges-Yangtze region, and possibly even as far as the present-day northern province of Shanxi, during the Late Quaternary period. Lǐ Báí's now famous poem (see page 18), written c. 756 A.D. during his trip home from exile through the Three Gorges to the Tang Dynasty capital Chang'an (Xi'an), alludes to this, describing gibbon song on the shores of the Yangtze River. There is now direct evidence that gibbons remained distributed this far north into the post-1500 A.D. historical period (Wen 2009, Chatterjee et al. 2012). However, since this time gibbons have suffered a severe contraction in their geographic distribution as a result of long-term deforestation and habitat destruction, and overexploitation including targeted hunting (Gao et al. 1981, Jiang et al. 2006, Zhang et al. 2010). Today, gibbons are found only in the south-western provinces of China: Yunnan, Guangxi and Hainan (Chivers et al. 2013).

As recently as 2006, China still supported the second-highest diversity of gibbons in the world (Grueter et al. 2009a), with six species of gibbons in three genera recorded (*Hylobates lar, Nomascus concolor, N. nasutus, N. hainanus, N. leucogenys, and Hoolock leuconedys*; Geissmann 2007). However, it now appears that *H. lar* has been lost from its last stronghold in China (Grueter et al. 2009a), and *N. leucogenys* may also be extirpated, with no records of the species in China since 1990 (Bleisch et al. 2008a) despite recent intensive survey efforts (Fan and Huo 2009, Fan et al. 2013a). Consequently, only four gibbon species persist in China: *N. concolor, N. hainanus, N. nasutus,* and *H. leuconedys*. Tellingly, these species comprise the

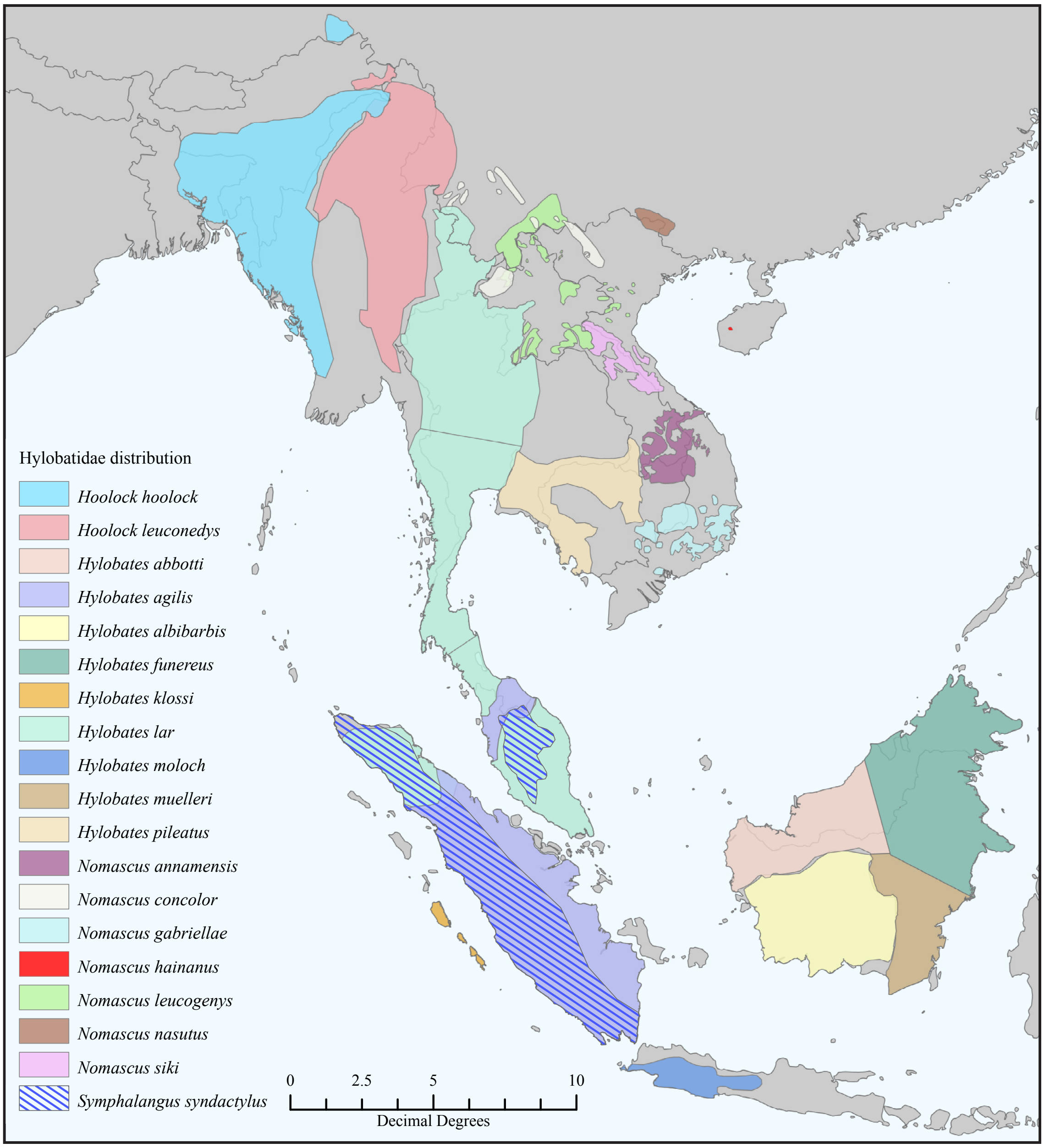


Figure 1.1 Map of the global distribution of the 19 recognised species of gibbon, Family Hylobatidae (after Thinh et al. 2010b, Rowe and Myers 2011, Chivers et al. 2013, IUCN 2013).

four Critically Endangered members of the gibbon family, and in fact, gibbons represent around half of the Chinese mammal fauna listed in this IUCN category (IUCN 2013). *Nomascus hainanus* is the only endemic Chinese gibbon. Alarmingly, this species and the Cao Vit gibbon (*N. nasutus*) are now reduced to just one extremely small population each, with highly restricted distributions (Mootnick et al. 2012). Until recently, *N. nasutus* was feared extinct, but was rediscovered along Vietnam's remote northern border in 2002 (La et al. 2002), and then across the border in China in 2006 (Chan et al. 2008), with a current trans-boundary population estimated at 110 individuals persisting in an isolated area of limestone forest (Dat et al. 2008). Fewer than 200 *H. leuconedys* individuals, in approximately 40 groups, are restricted to an area west of the Salween River in Yunnan (Fan et al. 2011b). There are also serious concerns for the *N. concolor* populations previously known in far south-western Yunnan, with populations now confirmed in only four areas (Bajiaohe, Yongde, and Wuliang Mountain and Ailao Mountain National Nature Reserves; Ni and Jiang 2009, Ni et al. 2014) and nothing known of the survival of populations in nearby areas (Changyuan, Zhengkang, Yunxian and Genma; Fan Peng Fei pers. comm., June 2013). A limited number of *N. concolor* and *H. leuconedys* populations exist outside China. Logging, agricultural encroachment, infrastructure development, illegal hunting, limited forest availability and population fragmentation continue to threaten the survival of all four of these species within China (Fan et al. 2009, Fan et al. 2011a, Fan et al. 2011b, Mootnick et al. 2012, Ni et al. 2014).

The Hainan gibbon

The Critically Endangered Hainan gibbon (*N. hainanus*, Figure 1.2) is not only the sole extant Chinese gibbon species, and the rarest gibbon species globally, but also the world's rarest ape, and one of the world's most threatened mammals (Mittermeier et al. 2007, Geissmann and Bleisch 2008, Baillie and Butcher 2012). Only a single wild population of around 25 individuals remains, restricted to approximately 15 km^2 of highly fragmented, suboptimal forest in Bawangling National Nature Reserve (BNNR), Hainan Island, China (Figure 1.3). Historical reports indicate the species was once widespread across Hainan, to which it is endemic, but experienced a severe and precipitous decline from the mid-twentieth century onwards, as a result of extensive, ongoing habitat loss in concert with targeted poaching for traditional medicines (Chan et al. 2005). BNNR was gazetted in 1980 to protect the gibbon and its habitat, and the species was afforded national protection in 1988 (under the Chinese Wildlife Protection Law), and listed under international law (IUCN) by 2003 (Geissmann and Bleisch 2008). However, despite these formal protection measures, and an apparently normal birth rate (Fellowes et al. 2008), the species has shown little population growth. The sole surviving population has fluctuated between approximately 10-25 individuals for almost thirty years (e.g. Liu et al. 1989, Zhang and Sheeran 1993, Wu et al. 2004, Zhou et al. 2005, Li et al. 2010). This

a)

b)

Figure 1.2 Hainan gibbon (*Nomascus hainanus*) a) mature male, and b) mature female with infant.

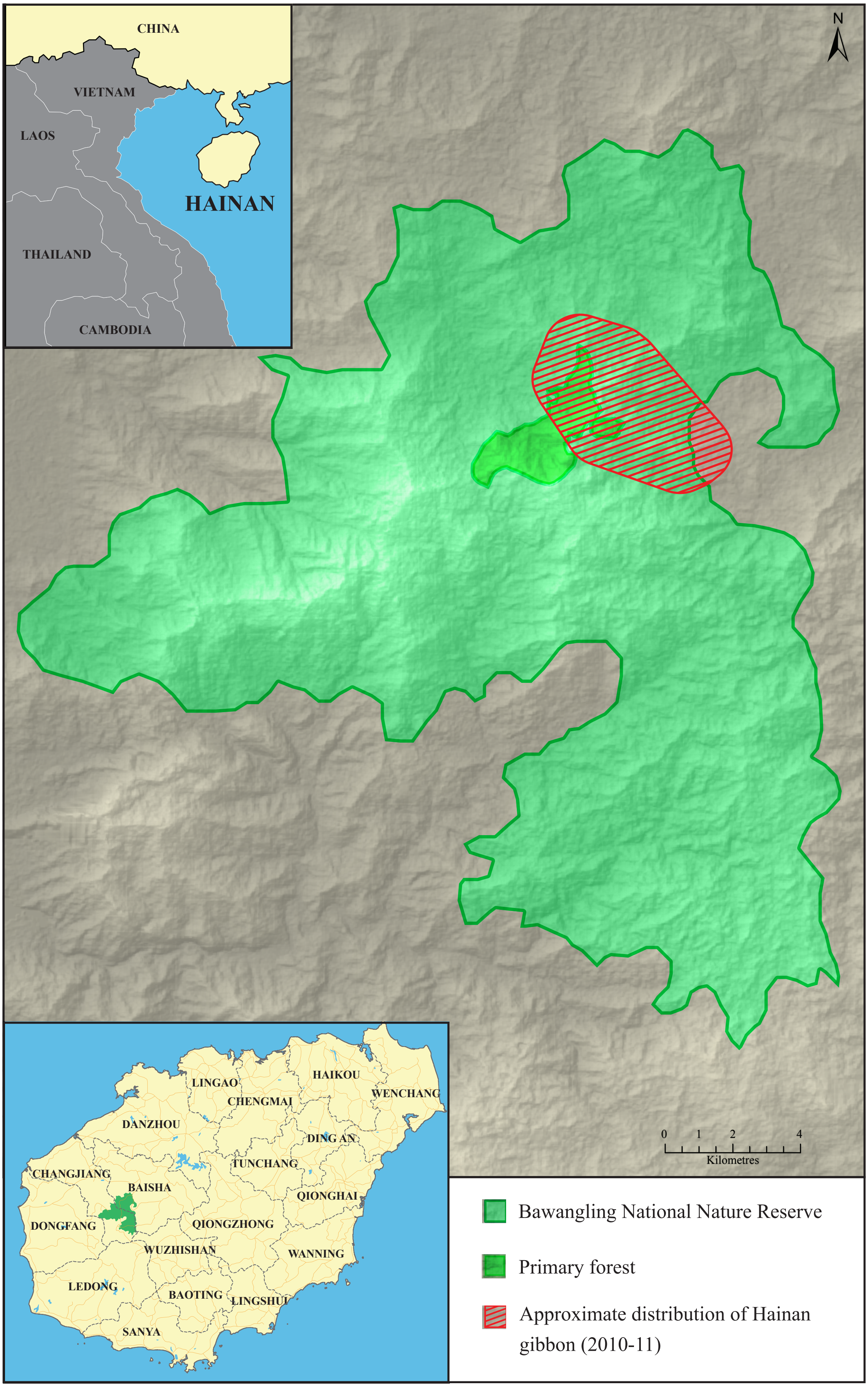


Figure 1.3 Location map showing current distribution of the Hainan gibbon; one population within Bawangling National Nature Reserve (BNNR), Hainan Island, China.

lack of growth raises serious concerns for the survival of the species. The continued low population size makes the species vulnerable to stochastic processes, Allee effects, and may have genetic implications (e.g. inbreeding) which will likely impact the species' long-term viability. There are no captive Hainan gibbons, meaning that the loss of the BNNR population would not only signify the species' extirpation from China, but the global extinction of the species, and the first known extinction of any ape species in the Holocene period.

As has been the case for other species of extreme rarity (e.g. Californian condor *Gymnogyps californianus*, black-footed ferret *Mustela nigripes*, Mauritius parakeet *Psittacula echo*), long-term recovery of the Hainan gibbon is likely to require intensive, carefully planned conservation. As previously argued, successful conservation of such species requires an in-depth understanding of both the causes behind the species' decline (usually extrinsic threats), and the intrinsic factors that will determine the species' population growth (problems associated with small population size, Allee effects etc.) (Caughley 1994). The direct extrinsic threats to the Hainan gibbon have been identified, but despite three decades of research into the BNNR population, relatively little is empirically known about the biology, ecology, and behaviour of the species. There have been reports of purportedly 'atypical' gibbon ecology and behaviour in the last remaining Hainan gibbon population at BNNR (Liu et al. 1987,1989, Liu and Tan 1990, Wu et al. 2004, Chan et al. 2005, Zhou et al. 2008a,b, Li et al. 2010), but many findings from past studies are clouded by a largely unsystematic approach or unclear reporting of methods used, creating uncertainty about even the species' basic biology. Consequently, the role of different intrinsic factors (ecology, genetics) and their interaction with extrinsic conditions (available habitat etc.) as potential constraints to the recovery of the population are not well understood. Management action to date has focused on monitoring and protecting the remaining population, and long-term landscape-level restoration of the BNNR habitat. Assumptions are being made about the likely factors behind poor population growth for which there is presently little systematically-obtained supporting evidence. Furthermore, there has been little incorporation of available quantitative decision-making tools into conservation planning.

Thesis aims and overview

The conservation of the Hainan gibbon represents one of the most urgent priorities for mammal conservation at a global level. However, the existing evidence-base for conservation planning remains severely inadequate, making it extremely difficult to assess what the most appropriate recovery actions may be for the population. New comprehensive baseline data are urgently required if appropriate management actions are to be identified, evaluated, and implemented to prevent the imminent extinction of this species. In this thesis I aim to provide a sound evidence-base for the Hainan gibbon, using a rigorous, objective, and systematic approach, to directly inform conservation management planning for the species. To achieve this, I adopted a multifaceted approach to satisfy three principle aims:

i) To clarify key features of the species' biology (ecology, behaviour, and population genetics);
ii) To evaluate the relative influence of a subset of factors (spatial requirements, genetic, ecological and behavioural factors) that may limit the population's potential for recovery;
iii) To determine the viability of the population in its present situation and predict how this might alter under possible recovery actions.

The findings of all aspects of my research therefore have immediate implications for the conservation management of the Hainan gibbon.

The first step in applying an evidence-based conservation approach is to review the existing evidence such that knowledge gaps may be identified. Therefore, in **Chapter 2**, I collate and critically evaluate the available information for the Hainan gibbon to clarify the extent of our current knowledge of the species based upon empirical data. This review thus provides a detailed background to the species, its recent population dynamics, and the problem of, and issues impeding, Hainan gibbon conservation.

The next two chapters directly investigate two specific components of the species' biology that have important implications for the recovery of the last remaining population and have been advocated as likely constraints to population growth, but for which little robust information exists. In **Chapter 3** I systematically evaluate the spatial requirements of the Hainan gibbon and the extent to which this factor may account for limited growth of the population to date, or be regarded as a priority for management of the population. In **Chapter 4** I comprehensively investigate the present genetic condition of the surviving population within the context of the species' past genetic diversity, to evaluate any genetic consequences of the past population bottleneck and implications for the long-term viability of the species.

The direct investigation of these two intrinsic factors is supplemented by a broader assessment of the ecological and behavioural characteristics of the species informed by contextual data for other gibbon species. In **Chapter 5** I use a comparative approach to investigate key Hainan gibbon traits by assessing potential drivers of observed variation in these traits across the Hylobatidae. This allows me to evaluate whether these attributes are phylogenetically constrained, or controlled by external factors in response to the population's current threatened situation.

In **Chapter 6** I employ a quantitative conservation planning tool (Population Viability Analysis) to assess the viability of the remaining population. By predicting the likelihood of extinction of the species in response to different threats, and under different management scenarios, I identify key limiting factors for the species' recovery and evaluate possible conservation strategies.

The final chapter, **Chapter 7**, summarises my thesis findings. Within this chapter I consolidate the findings of my different analyses to highlight factors of particular concern and relevance to Hainan gibbon recovery, and discuss the implications of these findings for conservation management of the sole surviving Hainan gibbon population and other species of extreme rarity.

Chapter 2. A conservation conundrum: the world's rarest and most poorly understood ape?

Introduction

> "[Hainan gibbons] are on the verge of extinction…efficient measures are urgently needed to save this endangered ape." (Liu et al. 1984, pp. 1-4)

In 1984, Liu and colleagues called for the urgent conservation of the Hainan gibbon, which they estimated to then number a total of 30-40 individuals (Liu et al. 1984). Unfortunately, thirty years later the species' situation remains just as precarious. In 2014, the Hainan gibbon is still Critically Endangered and continues to be the world's most endangered ape, with population numbers presently estimated at around 25 individuals, constituting three social groups (known as Groups A, B, C) and a small, unknown number of solitary individuals (BNNR Management Office pers. comm., March 2014). In 2003, a conservation planning meeting was held to formulate a conservation strategy for the species, and a Conservation Action Plan was produced in 2005 based on the conclusions and recommendations from that meeting (Chan et al. 2005). However, virtually no intensive conservation management of the surviving population has yet been employed, with action to date having focused on monitoring and broader landscape-level management, including campaigns to raise public awareness, as recommended by the action plan. As I will demonstrate here, this is largely due to a lack of systematically-derived information precluding an accurate appreciation of even the species' basic biology and ecology, which has prevented the identification of urgently required conservation actions.

A systematic review of existing evidence is fundamental to the evidence-based approach to conservation. Available information must be collated and evaluated to: a) afford assessment of the evidence for potential management actions in a comprehensive and objective manner; and b) identify knowledge gaps to allow prioritisation of research (Pullin and Knight 2003, Stewart et al. 2005). This approach has been an invaluable tool for the direct identification of appropriate conservation management actions (e.g. for ecological communities in the United Kingdom, see Stewart et al. 2005). The 2005 Hainan gibbon Conservation Action Plan brought together existing data for the species and identified research needs and potential constraints to the population's recovery. However, this report largely accepted the findings of past work as given, rather than evaluating the evidence to support previous claims about the species' biology. Furthermore, this document is now almost a decade old, and since the 2003 workshop additional research into the species has been published and remains to be incorporated into wider management frameworks. A new, impartial, critical appraisal of the available information regarding the species' ecology, behaviour and population status is required to inform Hainan gibbon conservation planning.

This review therefore aims to provide an up-to-date compilation of all existing data for the Hainan gibbon, and to critically evaluate the research conducted to date. This process will clarify the extent of our current knowledge of the species based upon empirical data, and identify key knowledge gaps. In addition to providing a detailed background to the species and past conservation efforts, through this synthesis I also appraise the available evidence used to infer recent population trends, drivers of the species' decline, and possible constraints to Hainan gibbon recovery. By assessing the robustness of past data on the status and ecology of the species, I demonstrate that, despite a number of field studies of the last surviving population in BNNR spanning nearly three decades, relatively little is empirically known about Hainan gibbon biology when this work is critically evaluated, and conservation efforts for the Hainan gibbon cannot be improved until this deficiency is rectified through new research.

Previous Hainan gibbon research

In China, the gibbon has featured in literature for more than two thousand years, as a symbol of philosophical ideals and the mysterious link between man and nature (van Gulik 1967). The Hainan gibbon was perhaps first noted in the words of exiled poets such as Su Shi (also known as Su Dongpo; 1037-1101 A.D.), who was banished to Hainan during the Song Dynasty (between 1097-1100), then the outermost realm of the Chinese Empire (Schafer 2010), and wrote of gibbon song in the mountains (see page 33). In the West, the existence of the species was documented in the late 1800s (Swinhoe 1870, Thomas 1892), and initial observations were made of its physical form and habits from captive specimens housed at London Zoo in the early 1900s (Pocock 1905, Welch 1911). As a result of this relatively early discovery, the species has been incorporated into various assessments of gibbon phylogeny and taxonomy and consequently experienced several changes in its taxonomic status (as species/subspecies/synonym), from as early as Matschie (1893) to as recently as Thinh et al. (2010a, 2010c). In the interest of clarity, this review focuses on the literature directly relevant to the Hainan gibbon – its biology, ecology, conservation and status. Due to the dynamic taxonomy of the species, and the gibbon family more generally, there are a number of papers in the literature that discuss populations of "*Hylobates concolor hainanus*" from regions other than Hainan (e.g. Dao's 1983 study which describes "*H. c. hainanus*" in northern Vietnam). These studies have not been included here because these populations which occur outside Hainan are now understood to represent different species (e.g. *Nomascus nasutus*), and their inclusion would only serve to create confusion regarding *N. hainanus* biology.

柏家渡

柏家渡西日欲落
青山上下猿鸟乐
欲因新月望吴云
遥看北斗挂南岳

一梦愔愔四十秋
古人不死终未休
草舍萧条谁与语
香风欲过白蘋州

苏轼

Baijiadu

In Baijiadu the western sun longs to set;
From summit to valley, the verdant mountains sing with the music of gibbons and birds.
At the new moon, yearning for the clouds of Wu;
Distantly looking out upon the Great Bear hanging over Hainan's southern mountain.

Dreaming of a peaceful forty autumns;
Our ancestors do not die and have not rested.
In a desolate grass hut, someone has spoken;
The fragrant wind desires to pass by the sandbanks.

-Sū Shì, sometime between 1097-1100 A.D.

(free translation by Tim Jeffree)

This literature review brings together all currently available information pertaining to the Hainan gibbon. From an extensive search of the published literature (including Chinese journal publications), grey literature and other unpublished material, a total of 52 papers or reports were found to discuss the species. Approximately 35% of these present new data on the species, as opposed to merely discussing the situation of the species or presenting data already reported by other researchers. Unfortunately, several papers fail to adequately acknowledge the source of their reported figures, particularly for population estimates, which means the assessment is limited. Additionally, when compiling this comprehensive review it was necessary to translate a number of articles published in Mandarin Chinese. However, as my review of these studies is based upon translation by a number of native Chinese speakers, any inaccuracies of interpretation should be minimal.

To date only a handful of studies have directly investigated the Hainan gibbon. Field research into the species began with the work of Liu and colleagues in the 1980s, which provided the first insights into the species' biology and ecology, including basic behavioural and developmental descriptions, data on population size and structure (social group composition), home range requirements, and habitat composition and gibbon habitat preference within BNNR (Liu et al. 1984, 1989, Liu and Tan 1990). This was supplemented by the work of Zhou and colleagues, which delivered new estimates of population size and social group composition, revised figures of the home range size of the species, and provided further observations of the species' (intra- and inter-group) behaviour (Zhou et al. 2005, 2008a, 2008b). More recently, three smaller studies have provided new observations of the species' feeding ecology (Lin et al. 2006a, 2006b), documented the change in gibbon habitat across Hainan (Zhang et al. 2010), and provided limited information regarding the species' genetic diversity (Li et al. 2010). The remainder of the relevant literature (and a substantial proportion of the total) has focused on reviewing the status of the species and/or documenting population change, a logical priority and consequence of the species' critical situation, but therefore contributing little new information (e.g. Tan 1985, Tan and Poirier 1988, Zhang 1992, Zhang and Sheeran 1993).

Hainan gibbon taxonomy

When assessing the evidence-base for the Hainan gibbon, it is crucial to consider the taxonomy of the species, which has changed a number of times over the last 120 years. The species was first described as *Hylobates hainanus* by Thomas (1892), despite his reservations that it warranted the status of species ("With the exception of the Siamang all the so-called species of *Hylobates* are so closely allied to each other and differ by characters of such slight importance that they seem to be really hardly worthy of specific distinction"; Thomas 1892, p. 146) . Matschie (1893) concluded that *H. hainanus* was only a junior synonym of *H. concolor* (described by Harlan 1826), and Pousargues (1900) considered the type described by Thomas to be without doubt the same as *H. nasutus* (described by Kunkel d'Herculais 1884) and recommended synonymising the two. However, both Pocock (1905) and Welch (1911) subsequently supported recognition of *H. hainanus* as a distinct species based upon their respective examinations of living captive specimens, according to obvious physical differences and vocal characteristics. For example, detailed description of the species' distinctive crested hair ("On the forehead and crown of the head the hair...grows somewhat *à la Pompadour*, being erect on the crown"; Pocock 1905, p. 175), and song (Welch 1911), was considered distinct from other gibbon species the authors had observed (including the species then referred to as *Hylobates agilis*, *H. concolor*, *H. hoolock*, *H. lar, H. leuciscus*, and *Symphalangus syndactylus*).

Since these early observations of the species, the taxonomy of the Hainan gibbon and its position in the gibbon family tree have undergone further revision, as new incarnations of hylobatid phylogeny have been proposed following new insights into gibbon biology, morphology and behaviour, and the advent of more advanced analytical techniques. Despite landmark work by Schultz (1933), involving the first large-scale study of the morphological differences amongst the gibbons, from the time of Thomas' (1892) description of the species until the early 1970s, the view of gibbon systematics remained largely unchanged. Two genera were recognised: *Symphalangus* (Gloger, 1841) containing just the Siamang (*S. syndactylus*), and *Hylobates* (Illiger 1811) containing all other known gibbon species, although other authors (Kloss 1929, Miller 1933) suggested all species belonged to just one genus, *Hylobates*. Groves (1972) formally revised the family into one genus, *Hylobates*, with three pre-established subgenera: *Hylobates*, *Nomascus* (Miller 1933), and *Symphalangus*, based upon a comprehensive morphometric and karyotyping dataset, which revealed a different number of diploid chromosomes for each subgenus. Further karyology saw the addition of a fourth, pre-established subgenus *Bunopithecus* (Matthew and Granger, 1923) to the family (Prouty et al. 1983), supported by data on pelage and vocalisation variations (Marshall and Sugardjito 1986).

Only relatively recently have the four subgenera been elevated to genera (Roos and Geissmann 2001, Geissmann 2002b, Brandon-Jones et al. 2004), a classification which is now generally accepted following the revision of the name *Bunopithecus* to *Hoolock* by Mootnick and Groves (2005). Modern molecular techniques along with vocal analysis methods have led to a number of new descriptions of gibbon phylogeny (Garza and Woodruff 1992, Hayashi et al. 1995, Su et al. 1995, Zhang 1995, Hall et al. 1998, Roos and Geissmann 2001, Chatterjee 2006, Monda et al. 2007, Roos et al. 2007, Whittaker et al. 2007). There is still some debate regarding the phylogenetic relationships within the family (Mootnick 2006, 2010a, Thinh et al. 2010c), including within *Nomascus* (Roos et al. 2007, Mootnick and Fan 2011), but based upon the most recent and comprehensive inferred phylogeny (Thinh et al. 2010a), the recent description of a new species, *N. annamensis* (Thinh et al. 2010b), and elevation of two *Hylobates muelleri* subspecies to species (*H. abbotti* and *H. funereus*), 19 distinct species of gibbon are currently recognised (Chivers et al. 2013).

During this period, the position and nomenclature of the Hainan gibbon has altered numerous times. Despite its original species-level designation, the species was subsequently grouped into *Hylobates concolor* in the classification presented by Pocock (1927) as part of the subspecies of *H. c. concolor*, a view later supported by Delacour (1951). Simonetta (1957) referred to the Hainan gibbon as subspecies *H. c. hainanus*, as did Ma and Wang (1986). Under the new classification with four gibbon subgenera by Groves (1972), the species (as a subspecies of *H. concolor*) was moved to the subgenus *Nomascus*. It was subsequently regarded by some authors as a subspecies of the poorly-defined species *H.* cf. *nasutus* (Geissmann 1997) or *N. nasutus* (Wu et al. 2004), and for a time there was general confusion about what actually constituted *hainanus* (and *nasutus*), with the names *hainanus* and *nasutus* being used interchangeably for specimens from mainland China and North Vietnam (Geissmann 1989a, Groves and Wang 1990). Liu et al. (1984) argued for the subspecies distinction of the Hainan gibbon, describing differences in pelage colouration between adult Hainan gibbon females and black-crested gibbon females from Yunnan. Groves (2001) referred to *Nomascus hainanus* as a full species but did not provide detailed justification. As a result, the Hainan gibbon has been variously referred to as: *Hylobates concolor, Hylobates concolor concolor, Hylobates concolor hainanus, Hylobates hainanus, Nomascus* c.f. *nasutus hainanus,* and *Nomascus hainanus*. This constant revision has also created some confusion within individual studies regarding correct species identification, leading to observations of the Hainan gibbon which do not actually represent the species (e.g. a purported description of Hainan gibbon song based upon a pair of captive animals now know to be two other species; Haimoff 1984). Despite this past uncertainty, the Hainan gibbon is now regarded as a distinct species, *Nomascus hainanus*, based on genetic, morphology and vocal characteristics (Mootnick et al. 2007, Roos et al. 2007, Geissmann and Bleisch 2008, Long and Nadler 2009, Thinh et al. 2010a, Mootnick and Fan 2011). Mitochondrial cytochrome b analysis indicates that the species likely represents a basal member of *Nomascus*, having diverged from all other species over 3 million years ago (Thinh et al. 2010a). Unfortunately, this past confusion over the taxonomic status of the Hainan gibbon is also likely to have contributed to delays in prioritising conservation activities for the species.

Early observations of the species

The Hainan gibbon has been known to science since at least 1870, when Swinhoe gave a written account of a species of ‘Black Ape’ on Hainan Island based on descriptions from local gazetteers and reports made to him by island authorities and locals (Swinhoe 1870). Recorded as the “Wooyuen” (i.e. *wū yuán* 乌猿 or black ape) of Hainan, males being black and females white, Swinhoe reported a great difficulty in obtaining a live captive animal to inspect. He failed to observe any live animals (wild or captive) and had to be content with only a skull fragment and a pair of ulnae given to him by a local official in Nychow (South Hainan). In this early account Swinhoe provided some basic behavioural observations taken directly from a local gazetteer including the species' great agility in the canopy, along with "its love for climbing and its mild disposition" (Swinhoe 1870, p. 224). The species was formally described in 1892 based upon the first specimen of the species to be brought to Europe, donated to the British Museum (Natural History) after four years of captivity in mainland China in the care of a Mr W. T. Lay (Thomas 1892). Thomas' description provided little insight into the species beyond its general resemblance to the species then referred to as *Hylobates hoolock* but marked difference to this and all other gibbon species known at the time by the entire absence of the white superciliary streak.

The first basic observations of the species' biology were published in the early 20th century by Pocock (1905) and Welch (1911) from the study of three captive individuals of the species, two male and one female, housed within London Zoological Gardens during the period from 1892 to 1911. As remarked by Flower (1892), these were notable additions to the Zoo's menagerie. Key observations included a detailed description of the species' physical appearance, particularly the presence of erect hair on the crown of the head (Pocock 1905, Welch 1911), and the overall physique of the species as more slender in body and limbs than other species available for observation at the time (as specimen skins at the London Natural History Museum), including the then named *Hylobates agilis, H. lar, H. hoolock,* and *H. leuciscus* (Welch 1911). Pocock (1905, p. 173) provided what is likely the first published report of the ontogenic pelage colour change known in the species which he termed "canescence" and which he observed occurs at maturity in only females of the species, noting the "coincidence between the appearance of menstruation and that of the colour change" (see Figure 2.1). Also within these early observations is a clear description of the difficulty of sexing individuals before maturity (in the absence of the difference in coat colouration) as a result of the large, elongated peniform shape of the female external genital organs which could be mistaken for a penis (Welch 1911) and reportedly led to repeated mistakes on the part of Europeans in determining females as castrated males (Pocock 1905). For further details of the specimens upon which Thomas (1892), Pocock(1905), and Welch (1911) based their early observation of the species, see Appendix A. Beyond these notable observations, these early accounts serve mainly to place this species in the context of other gibbons known at the time, and provide only limited insight into the Hainan gibbon's specific biology and behaviour.

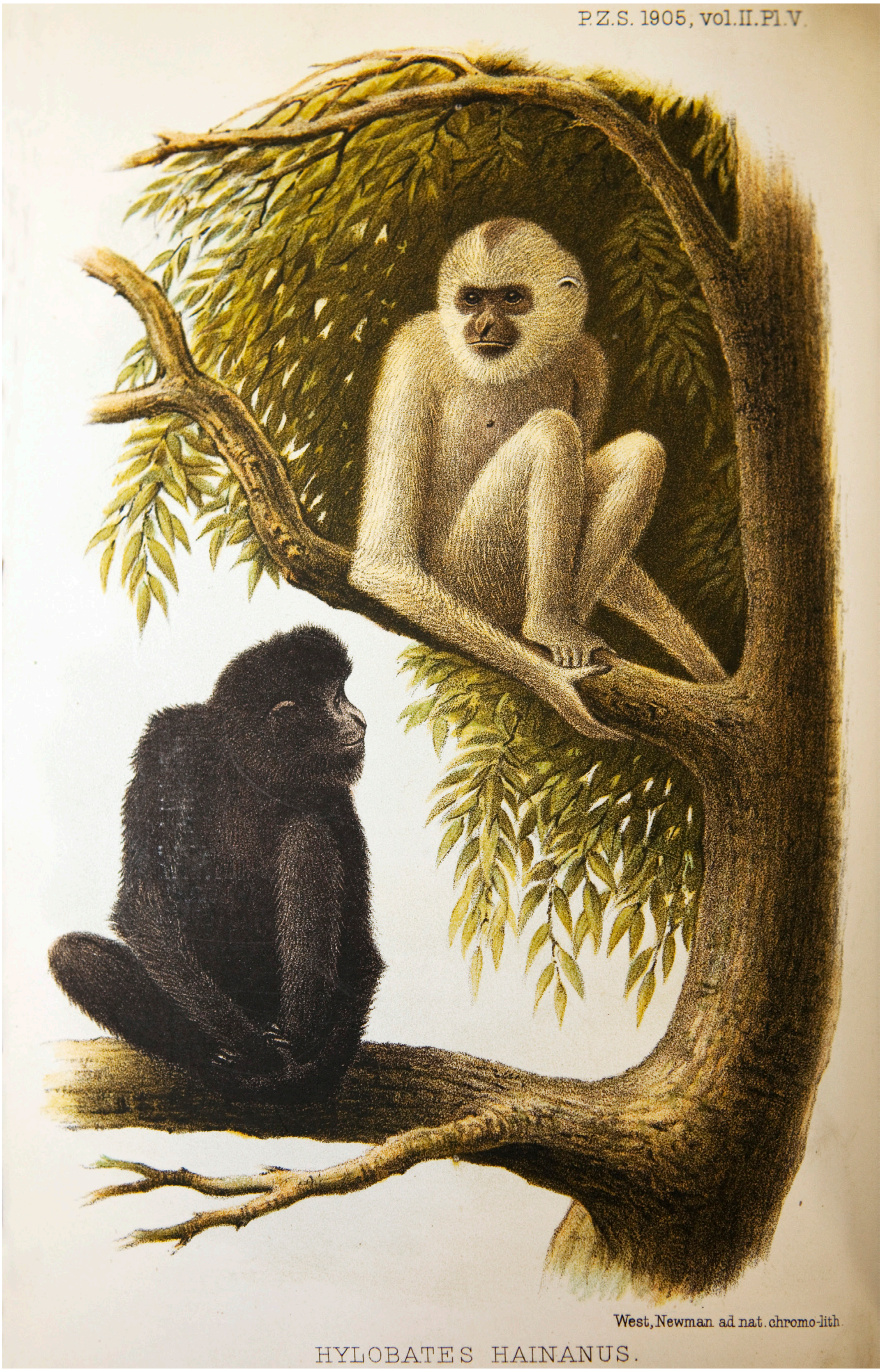


Figure 2.1 Illustrative rendering of the Hainan gibbon (then *Hylobates hainanus*) from Pocock (1905, p. 180) demonstrating the ontogenic pelage colour change that occurs in females; "from the female now living in the Society's Menagerie. The lower figure… represents the ape when she first came to the Gardens. The upper figure… shows her as she has been since the change of colour took place."

Hainan gibbon biology

In the following sections I assess the available evidence for characterising a number of key features of Hainan gibbon biology, behaviour and ecology, and highlight the issues associated with the studies to date that reveal a substantial level of uncertainty in many of the reported parameters. The references used to conduct these assessments are presented in Appendix B, which summarises past research investigating or discussing the biology, behaviour and/or ecology of the Hainan gibbon, or providing estimates of the species' population size.

Home range and spatial requirements

In total, nine papers have reported a home range figure for the Hainan gibbon (Appendix B), with estimates ranging from 2.00-9.87 km^2. All of these estimates appear to have been derived from two main bodies of work: Liu and colleagues for the period 1984-1989 (Liu et al. 1989, Liu and Tan 1990, Liu et al. 1995); and Zhou and colleagues for the period 2006-2008 (Fellowes et al. 2008, Zhou et al. 2008a, 2008b, Li et al. 2010). Liu et al. (1984) reported social groups to have a relatively fixed home range which is defended by the social group, but a range that will shift with season. Despite this description, and a basic indication of the locations of the different social groups with simple maps, the authors did not provide any estimates of home range size. The first home range estimate for the species was reported by Liu et al. (1989) as between 2-5 km^2. These authors also indicated that group ranges only 'moderately' overlap, but did not quantify the extent of overlap. Based upon the same work, Liu and Tan (1990) supported this estimate, but Liu et al. (1995) reported a home range estimate of c. 3 km^2. In this later paper, the authors also described the seasonal ranging of the species in terms of time spent in different areas in each season, but failed to break down the home range estimate given by season to elucidate any seasonal variation in the area utilised.

Crucially, based upon their 3 km^2 home range estimate, Liu et al. (1995) argued that the home range of the Hainan gibbon is 10 times larger than that of other gibbon species, specifically comparing this with the Yunnan black crested gibbon (*Nomascus concolor*). Quoting the home range figures from the studies of Liu and colleagues, Chan et al. (2005) contextualised these estimates by descriptively comparing them to those then available for both crested (*Nomascus*) and non-crested gibbon species, and concluded that the Hainan gibbon exhibits the largest home range of any gibbon species. This seemingly exceptional home range requirement has subsequently been used to explain the species' restricted population size within BNNR from the 1980s onwards. Liu et al. (1989) reported that the limited amount of available habitat within BNNR was probably close to limitation, with four social groups then recorded to be occupying a total of 12 km^2, while the most favourable habitat for the Bawangling gibbons was confined to only c. 15 km^2. Wu et al. (2004) supported this space-limiting theory and suggested that population growth was directly limited by a combination of human disturbance and available space: “The carrying capacity of the part of the reserve in which there are regular patrols is probably limiting the growth of the population” (p. 455). After the second major study into the species, Zhou and colleagues revised the species’ home range upwards considerably , with estimates of 4.38-9.78 km^2 (Zhou et al. 2008a), and 5.84-9.87 km^2 (Zhou et al. 2008b). These even larger estimates of home range provided additional evidence for the space-limiting theory, with Zhou et al. (2008b) arguing that there was no vacant suitable habitat for maturing gibbons to establish their own territories.

Clearly, an accurate understanding of the species’ spatial requirements is crucial to this theory of available habitat in combination with home range limiting the number of social groups that can form and thus the number of gibbons the reserve can support. Unfortunately, these arguments are based upon estimates of home range size that have not been qualified in terms of methodology. None of the reports of Hainan gibbon home range provide any information about the spatial analysis methods employed to calculate the estimates, and there is only minimal information about the effort used, meaning that it is also unclear what temporal period the estimates pertain to, whether the estimates provided are those of the species for a month, a season or a year, or how these requirements vary over seasons. It is even difficult to be certain of the exact estimates reported in the most recent study, which represent the largest estimates for this or any gibbon species. Inconsistencies between the estimates described in the papers of Zhou and colleagues limit confidence in these figures, with the home range of Group B changing from 4.38 km^2 to 5.84 km^2, and that for Group A seemingly inverted from 9.78 km^2 to 9.87 km^2 between Zhou et al. (2008a) and (2008b), and when subsequently re-reported by Fellowes et al. (2008). This may be either a transcription error or estimate revision based on improvements to the spatial analysis methods used or amount of data incorporated, but as these details are not reported in either paper, or any of the papers quoting these figures, it is impossible to know. The lack of disclosure of research effort or analytical approach for all reported estimates makes it difficult to critically evaluate any of the estimates published to date to determine how representative they are, or to accurately compare them to existing estimates for other gibbon species. Additional, methodologically-explicit investigation of the species’ home range is required to clarify if the Hainan gibbon’s spatial requirements truly differ from other gibbon species, and to what extent, and the role this ecological factor may play in regulating population growth within BNNR.

Feeding ecology

According to early observations, the Hainan gibbon diet reportedly consists of 119 plant species in 62 genera and 32 families, with 15 major fruiting trees providing the principal diet, but up to

40 ‘favourite’ species recorded (Liu et al. 1989, Liu and Tan 1990; Appendix B). Lin et al. (2006a) collated direct observations of plant species eaten by gibbons from long-term BNNR Management Office monitoring data to observe a diet of only 80 species in 59 genera and 40 families, noting a lower proportion of figs (c. 10%) than other gibbon species, and the absence of a number of species (e.g. from the Proteaceae and Fagaceae families) reported by Liu and Tan (1990), which was based upon observation of one group for 10 days every month over 12 months. This difference could indicate differences in accuracy of plant species identification or observation effort by the different research groups, a temporal shift in gibbon diet, or a change in forest quality producing a reduced abundance of these species over time. The latter explanation seems unlikely, however, as Lin et al. (2006a) indicated a high abundance of many of the previously recorded food trees which they did not detect as part of the Hainan gibbon diet. Given the suggestion that habitat condition within BNNR is a limiting factor for Hainan gibbon population growth and recent efforts to enhance and reforest areas through planting of gibbon food tree species (Chan et al. 2005), clarity regarding the exact composition of the diet will have important implications for any assessments of BNNR forest condition for Hainan gibbons (e.g. as per Lin et al. 2006b) and therefore management planning. Additional data collection (or reassessment of existing data) could assist in this regard and would also serve to inform analysis of factors underlying group ranging patterns.

Calling behaviour

Like other gibbons the Hainan gibbon produces a loud, elaborate morning call or ‘song’ with sex-specific components, which likely serve to promote social group cohesiveness and territory defence (Cowlishaw 1992). Starting immediately after dawn, when there is a peak singing period (06:00-07:00), additional songs occur at decreasing probability later into the morning and occasionally early afternoon (Chan et al. 2005). Song bout duration is reportedly between 5-35 minutes (Liu et al. 1984, Wu et al. 2004), as per most gibbon species (Geissmann 2002a). Pocock (1905) described the species’ call, based upon observations of a female captive individual, as consisting of about three to six distinct cries repeated in very rapid succession, followed by a momentary pause, after which the cry is repeated, representing it as “–hoo hoo hoo hoo – hoo hoo hoo – hoo hoo hoo hoo hoo – &c.” (with each ‘hoo’ given an ascending inflection in notation, p. 176). This is supported by the description of Liu et al. (1984), who indicated that the pace and pitch of the Hainan gibbon’s song increases steadily with each repetition, culminating in a sharp, high pitched end. Pocock’s (1905) description pertains to only the female portion of the song, while that of Liu et al. (1984) captures both the male and female phrases which, combined, produce a species-specific coordinated duet song, with a structure distinctive from other *Nomascus* species (Geissmann 2002a, Thinh et al. 2011). Despite the assertion that the species’ call had been recorded and analysed in a pair of captive specimens housed at Twycross Zoo, U.K. (Haimoff 1984), subsequent visual identification indicated the male was *N. concolor*, and the female *Nomascus leucogenys* (Andrew Kitchener pers. comm., June 2010), confirmed by genetic analysis (Christian Roos pers. comm., November 2011). Therefore, beyond Geissmann's (2002a) basic sonographic assessment, the Hainan gibbon song has not been analysed in depth, although songs have been used to aid field studies by permitting group location to be determined so that groups can be tracked (Liu et al. 1989, Liu and Tan 1990, Wu et al. 2004, Chan et al. 2005, Zhou et al. 2005, Zhou et al. 2008a, Zhou et al. 2008b).

Reproductive biology

Hainan gibbon individuals reach sexual maturity at c. 5-8 years of age after which they exhibit strong sexual dichromatism: males are black and females are light yellow except for a dark occipital patch (Liu et al. 1989). As first observed by Pocock (1905) in a captive female individual, and then by Liu et al. (1989) in wild individuals, ontogenetic changes in fur colouration are pronounced. Infants are born with light colouration similar to adult females; at approximately one year the coat becomes black, resembling adult male colouration. At the age of sexual maturity females change colour again to the light yellow colour typical of adult females, while adult males remain black (see Figure 1.2). Due to a lack of dichromatism or obvious difference in the appearance of external genital organs, it is extremely difficult to determine the sex of immature individuals based solely on visual observations.

An estimate of the species' breeding rate was initially reported by Liu et al. (1984) as one offspring every 2-3 years. This was subsequently revised to one infant per adult, reproductive female every two years or an inter-birth interval (IBI) of 24 months (Fellowes et al. 2008, Zhou et al. 2008b). Liu et al. (1989) provided records of new births for the four social groups that persisted between 1982-1987. However, despite the assertion of Zhou et al. (2008b) and Fellowes et al. (2008) that these data support an IBI of 24 months, failure by Liu and colleagues to provide sufficiently detailed information to assign observed births to individual females limits the accuracy of the resultant estimate of the species' birth rate. Data supporting a rate of new infants being produced every two years have been provided by long-term monitoring data collected by BNNR Management Office staff between 1996-2007, which form the data presented by Zhou et al. (2008b) and Fellowes et al. (2008). When combined, the BNNR data provided in these two studies spans 10 years, and although there is limited information supplied to clarify the exact birth rate per adult female (beyond all Group B births being attributable to one female whose identity has apparently not changed over this time; BNNR Management Office pers. comm., March 2014), the data nonetheless reveal an overall birth cycle of two years (Table 2.1). This is slightly less than that reported for other gibbon species, generally estimated

Table 2.1 Hainan gibbon births 1996-2007, as reported by Fellowes et al. (2008) and Zhou et al. (2008b).

Social group	**Month and Year of birth**	**Number of births (after Fellowes et al. 2008)**	**Reference(s)**	**Notes**
Group A*	October 2003	1	Fellowes et al. (2008), Zhou et al. (2008b)	
* 2 adult females known since at least 1997 according to Zhou et al. (2008) but only births of ‘A2’ reported: 2003, 2005.	April 2005	2	Fellowes et al. (2008)	reported as 1 birth only (by ‘A2’) in January 2005 by Zhou et al. (2008b)
	March 2007	2	Fellowes et al. (2008)	
Group B[$]	September 1996	1	Zhou et al. (2008b)	
[$] All births can be attributed to ‘B2’, the only reproductive female in Group B during this period whose identity has not changed during this time (BNNR Management Office pers. comm., March 2014)	June 1998	1	Zhou et al. (2008b)	
	2000	1	Zhou et al. (2008b)	no month specified
	November 2002	1	Fellowes et al. (2008), Zhou et al. (2008b)	
	December 2004	1	Fellowes et al. (2008), Zhou et al. (2008b)	
	January 2007	1	Fellowes et al. (2008)	

at three years, e.g. *Hoolock hoolock* (Molur et al. 2005), *Hylobates lar* (Tunhikorn et al. 1994), *Hylobates klossii* (Tilson 1981), *Hylobates agilis* (Mitani 1990), and *N. annamensis* (Chivers et al. 2013). There have been suggestions that the observed breeding cycle is linked to the phenology of the habitat, with births apparently coinciding with mast fruiting of key food trees *Litchi chinensis, Nephelium topengii*, and *Ficus glaberrima* (Chan et al. 2005, Zhou et al. 2008b), but there remains little direct evidence and no systematic statistical evaluation to support this assertion.

Extended observation by Zhou et al. (2008b) also allowed estimation of a number of other reproductive parameters, including: gestation period (136-173 days); time to independence of infants (1.5 years); and age at emigration for maturing offspring (c. 5.5 years). Reproductive behaviours were also revealed, e.g. all observed mating events were initiated by females. However, general conclusions from this work must be treated with caution, as virtually all of the estimates of reproductive and developmental parameters provided by Zhou et al. (2008b) are based upon one observation for each given parameter. Despite this, gestation period at least seems to be in keeping with other gibbon species, with Geissmann (1991) reporting a period of approximately 7 months in captive *N. leucogenys* and similar estimates for other captive *Hylobates* species and *Symphalangus syndactylus*. Clearly we must accept some level of uncertainty when estimating Hainan gibbon population parameters, and employ the current estimates, at present the best available, with caution.

Social group size and emigration of offspring

Conventionally, it has been understood that gibbon social groups consists of an adult male, an adult female, and up to three offspring, which are evicted from the natal group at maturity to establish their own breeding pair and social group (Bartlett 2007, Chivers et al. 2013). This view is based upon long-term studies of *Hylobates* species, from the studies of Carpenter (1940) onwards. More recent evidence from *Nomascus* species suggests that gibbon group size may be more plastic than this. *Nomascus hainanus* group size has been observed to be anywhere between 3-12 individuals (Wang 1995, Wu et al. 2004, Li et al. 2010), with an average of between 5-7 individuals most commonly reported (Liu et al. 1987, Liu et al. 1989, Wu et al. 2004, Chan et al. 2005, Zhou et al. 2008a, Zhou et al. 2008b; Appendix B). It is difficult to be confident in the accuracy of several of these figures given the general lack of disclosure in many studies regarding the methods and effort employed to calculate group size estimates. However, these figures do align with estimates reported for other crested gibbons. *Nomascus nasutus* group sizes appear to be similarly ‘larger’ than the general *Hylobates* description, ranging from 5-6 individuals in Cao Bang, Vietnam (Geissmann et al. 2002), and 3-8 individuals in Guangxi, China (Chan et al. 2008, Fei et al. 2012), and *Nomascus concolor* groups reportedly range from

3-10 individuals, containing 5-6 individuals on average (Haimoff et al. 1986, 1987, Sheeran 1993).

Together, these group size estimates could either indicate an evolutionary difference between crested versus non-crested gibbons, or, as has been postulated elsewhere (Chan et al. 2005, Zhou et al. 2008b), a response of these species to reduced habitat availability and suboptimal habitat quality, with such conditions possibly preventing establishment of new social groups and forcing individuals to remain within their natal groups. Emigration of offspring from natal groups has been documented only anecdotally for the Hainan gibbon. Zhou et al. (2008b) reported one direct observation of the eviction of a subadult male from Group B at approximately 5.5 years of age following regular observations of the adult male of the group pursuing him. Additionally, Fellowes et al. (2008) reported that a single individual departed from each group in the period 2002-2007, indicating that at least some maturing individuals have left social groups. However, the fate of such individuals is unclear, with solitary individuals being particularly difficult to locate due to their tendency to rarely call and the general difficulty of tracking gibbons in the mountainous habitat of BNNR (Chan et al. 2005, Fellowes et al. 2008). The intrinsic versus extrinsic drivers of differential gibbon social group size remain to be assessed through a detailed comparative analysis across the gibbon family.

Social group structure: a polygynous mating system?

The mechanisms driving Hainan gibbon social group dynamics are also not well understood. Multiple observations of the BNNR population over the last three decades indicate a polygynous social group structure, with Liu et al. (1987, p. 50) first documenting an “unusual composition of one adult male and two adult females”, and additional accounts supporting this description in the intervening years (Liu et al. 1989, Bleisch and Chen 1991, Wu et al. 2004, Zhou et al. 2008b). This is not the first report of a polygynous group structure in gibbons; Delacour (1933) and Haimoff et al. (1987) both described groups of *N. concolor* containing multiple adult females. However, suggestions of polygyny in gibbons have generally been met with scepticism (Groves 1972), as many such reports have generally lacked direct evidence of more than one female breeding in a given group, an inadequacy often, and rightly, employed to doubt the presence of polygyny (Bleisch and Chen 1991). In light of this, a critical review of the available evidence provides only limited direct support for polygyny. The only data presented in support of two females giving birth within a social group is that of Liu et al (1989), who indicated that they were not able to confirm polygamous mating, but the observed age structure suggested that it had occurred. Subsequent reports claiming to ‘confirm’ this polygyny in the Hainan gibbon (Wu et al. 2004, Zhou et al. 2008b) have largely lacked evidence beyond observations of more than one adult female within each social group. This is not to suggest that the Hainan gibbon does not display a polygynous mating system, but that an in-depth assessment of the existing evidence-base reveals this to be yet another facet of the species' behaviour which remains unclear as a result of a lack of defensible data.

In an attempt to reconcile the purported polygyny of the Hainan gibbon with the conventional, often "uncritical acceptance" of gibbon monogamy (Palombit 1994, p. 83), it has generally been argued that this mating strategy is a response to the population's critical situation. Reduced available habitat and/or low habitat quality within BNNR in combination with large home range requirements, as well as small population size leading to a lack of potential mates for new mating 'pairs', have been cited to explain the observation of individuals remaining within their natal groups and the apparently polygynous mating system (Liu et al. 1989, Bleisch and Chen 1991, Jiang et al. 1999, Wu et al. 2004, Zhou et al. 2008b). Polygyny, as confirmed through observation of multiple females supporting infants within one social group, has also been observed in *N. nasutus* in Guangxi (Chan et al. 2008, Fan et al. 2010), and similarly for *N. concolor* (Jiang et al. 1999, Fan et al. 2006), with at least one study observing long-term (>6 years) polygynous groups in the Wuliang Mountains, west-central Yunnan (Fan and Jiang 2010). *Nomascus nasutus* and *N. concolor* are also listed as Critically Endangered (Bleisch and Geissmann 2008, Bleisch et al. 2008b), with *N. nasutus*, like the Hainan gibbon, suffering a greatly reduced population size and limited available habitat (Mootnick et al. 2012). These observations could therefore support a 'disturbance' theory for polygyny. Alternatively, the probable manifestation of this social structure in the sister species *N. hainanus* and *N. nasutus* and the closely related *N. concolor* may also point to this trait being a characteristic common to *Nomascus*, or at least these basal *Nomascus* members (see phylogenies in Roos et al. (2007) and Thinh et al.(2010a)).

Evidence of poylgyny has also been documented in *Hylobates lar* (Sommer and Reichard 2000), *Hylobates pileatus* (Srikosamatara and Brockelman 1987), including hybrid *lar-pileatus* groups (Brockelman and Srikosamatara 1984), and *Hoolock hoolock* (Ahsan 1995), although these observations of polygynous groups were all short-term (each lasting only several months). To confuse matters further, instances of 'socially polyandrous' groups of *H. lar*, comprising an adult female, adult male and a second unrelated adult male have also been observed in Khao Yai National Park, Thailand (Barelli et al. 2007). Evidently, gibbon group structure and mating strategy are clearly more complex than early studies suggested, with questions regarding the possibility of facultative versus obligate monogamy, and transient monogamy versus 'life-long' pair-fidelity remaining unresolved due to a general lack of longitudinal data on the reproductive activity of individual gibbons (Palombit 1994). For the Hainan gibbon, despite thirty years of observation, like virtually every other uncertainty regarding the species' biology, a current lack of systematic data precludes any firm conclusions from being drawn regarding the potential polygyny displayed or the mechanisms behind this purported social structure.

Genetic characteristics

Genetic study of the Hainan gibbon has largely consisted of its inclusion as a species or subspecies in gibbon phylogenetic analyses based upon morphometric, vocal, and molecular data (Su et al. 1995, Zhang 1995, Thinh et al. 2010a). Despite the species' demonstrated genetic distinctiveness and significance as basal within *Nomascus* (Thinh et al. 2010a), virtually nothing is known of its genetic characteristics or, crucially, the population genetics (diversity, intra- and inter-social group relations, level of inbreeding etc.) of the surviving population. Several authors have alluded to the potential genetic consequences of a greatly reduced population size and have argued that the surviving population is likely to be suffering from genetic constraints including inbreeding and reduced genetic diversity (Liu et al. 1989, Zhou and Zhang 2003, Fellowes et al. 2008). However, only one study has actually attempted to investigate the genetic diversity of the species: Li et al. (2010), who assessed the population's haplotype and nucleotide diversity using the mitochondrial D-loop sequence. Unfortunately, there are a number of drawbacks to this work which limit confidence in the study findings and thus their utility.

Sampling limitations meant that the authors sampled and sequenced only six individuals from one of the then two existing social groups, severely constraining any conclusions regarding the species' current level of diversity. The diversity observed was compared to that of two other endangered primates, the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) and Sichuan snub-nosed monkey (*Rhinopithecus roxellana*), leading the authors to state that the Hainan gibbon's haplotype diversity and nucleotide diversity are low (Li et al. 2010). However, they failed to contextualise their results in terms of other gibbon species' genetic diversity, or the historical diversity of the Hainan gibbon, therefore preventing clarity about whether the observed levels of genetic diversity are truly lower, or rather characteristic of the family, the *Nomascus* clade, or even the species (alluding to long-term reduced diversity). Apparent issues associated with possible sequencing errors also limit the utility of the results. Four mitochondrial DNA haplotypes were reported within one social group, leading the authors to conclude that the group showed no inbreeding (Li et al. 2010). Extended population data for this group from nearly nine years of monitoring indicated, according to the authors, that three juveniles within the group were the offspring of the breeding adult female, and only one other non-breeding adult female (purportedly the mother of the breeding female) and one breeding adult male existed within the group. This would suggest far fewer haplotypes than reported, pointing to probable methodological errors. As such, only limited insights regarding the remaining Hainan gibbon population's genetic condition can be gained from this work. Further, careful and comprehensive assessment of the species' genetic diversity, the relatedness of remaining individuals, and any evidence of inbreeding within the population, is urgently needed to resolve concerns regarding the genetic consequences of small population size, including the implications for population viability.

Hainan gibbon conservation

Current distribution and population composition

In 2014, only a single surviving population of *N. hainanus* within BNNR is known to exist. Surveys in 2003 failed to locate any populations outside BNNR (Chan et al. 2005), and ongoing efforts to detect any as-yet-unknown surviving populations in nearby reserves have been unsuccessful (Bosco Chan pers. comm., March 2014). In addition to there being no other known wild populations, there are no known records of any captive Hainan gibbon individuals, despite search efforts. Geissmann's recent census of captive gibbons in the South East Asian region produced no records of *N. hainanus* in zoos or institutions in China, or the surrounding region, from a total of over 60 captive gibbon individuals discovered in 12 separate institutions surveyed (Geissmann 1995). It is possible, but highly unlikely, that some individuals could persist in private zoos or collections in China or surrounding countries. However, obtaining information on such collections, which would constitute illegally kept animals, is particularly difficult. Consequently, there is no reliable captive population upon which conservation actions such as captive breeding could be based, and efforts to conserve the last remaining wild population within BNNR will represent the sole opportunity to conserve the species.

The sole surviving population currently numbers an estimated 25 individuals, constituting three social groups – Groups A, B and C, the last of which emerged during the course of this study in 2011– and up to four solitary individuals (this study; BNNR Management Office, pers. comm., March 2014). The population is restricted to around 15 km^2 of suitable but highly fragmented, sub-optimal forest within BNNR (Liu et al. 1989, Chan et al. 2005) –see Figure 1.1, Figure 2.2. Established in 1980, the reserve is located at 18°57'–19°11'N, 109°03'–109°17'E, and at almost 300 km^2 in total, straddles two counties (Changjiang and Baisha Li Autonomous Counties). The vegetation within the reserve is made up of lowland and montane/ravine rainforest, and evergreen broadleaf forest (Zhang et al. 2010), but the gibbon population now appears constrained to relatively high elevation habitat between 800-1,200 metres above sea level (m a.s.l.; Chan et al. 2005, Fellowes et al. 2008). The climate in BNNR is tropical seasonal with a mean annual temperature of 21.3 ºC (minimum in December with mean of 15 °C, and maximum in June with mean of 22.5 °C), mean annual rainfall of 1,660 mm and mean relative humidity of 88.6% (Chan et al. 2005).

Figure 2.2 View of BNNR showing existing global Hainan gibbon range extent, comprising mid-high elevation forest on slopes of mountain ridges in distance.

The decline of the Hainan gibbon

Several reports indicate that the Hainan gibbon originally occurred across Hainan Island but suffered a precipitous decline in the middle of the 20th century. Zhang et al. (1981) in their summary of the status of primates in China reported the occurrence of "*H. concolor*" on Hainan Island and highlighted a decline in *Hylobates* spp. in the south China region generally, indicating that this and other primate species in the region were already threatened with extinction. The authors indicated that "*H. concolor*" (presumably *N. hainanus*) was then restricted to Jianfengling and Bawangling Nature Reserves in Hainan, each less than 2,000 km^2. However, Zhang et al.'s (1981) report of the threat of extinction was not specific to the Hainan gibbon and did not detail the situation of gibbons in Hainan.

The drastic decline, and consequent critical situation of the species, was first recorded by Liu et al. (1984). This paper presented a putative historical distribution of the species, reporting that in the 1950s gibbons were distributed in 12 counties across the island and, based on figures provided by local hunters in six of these regions, extrapolated that the total population likely numbered more than 2,000 individuals at that time. This estimate has since become the baseline for discussion of Hainan gibbon population decline, with almost every paper written about the

Hainan gibbon after 1984 citing this figure (e.g. Tan 1985, Wu et al. 2004, Chan et al. 2005, Fellowes et al. 2008). It is unfortunate, therefore, that a figure which is so widely quoted and so pivotal to demonstrating a marked pattern of decline for the species is at its origin so imprecise, but it stands as the only historical estimate of past population size for this period.

Other sources also support a greater past distribution. In his early accounts Swinhoe (1870) reported the occurrence of gibbons in regions across Hainan: namely Central ('Taipingsze'), Southern ('Nychow'), and South East ('Lingshuy') Hainan, though he himself failed to observe either wild or captive animals in any of these locations. More recently, Zhou et al. (2005) also supported a wide historical distribution based upon information on the species' historical occurrence collected through community interviews and access to local government resources, and described a contraction of Hainan gibbon range across Hainan from 1688 to 2003, with the most marked reduction (in distribution and number) between the 1950s and the 1980s. Compilation of historical gazetteer records (*dìfāngzhì*) by Wen (2009) provided further gibbon last-occurrence records for other counties across Hainan for which Zhou et al. (2005) did not provide data (see Table 2.2). Accounts from other authors confirm that the species had already been lost from Jianfengling Reserve by the late 1980s (Tang 1987), and by 1989 the population was reportedly diminished to only 21 gibbons in four groups restricted to just BNNR (Liu et al. 1989). In 2003 only 13 gibbons were recorded in the first comprehensive status survey for the species (Chan et al. 2005). Together, these accounts indicate a clear, although not precisely quantifiable, decline in the abundance and distribution of the Hainan gibbon over the last century –see Figure 2.3.

Assessing population trends

Since Liu and colleagues' call to arms in 1984, there has been a tendency for reviews to assess the species' status, usually involving estimation of population size. Every reference in the available literature to estimate Hainan gibbon population size to date is catalogued in Appendix B. By compiling population estimates from these papers it is possible to observe broad population trends, including the abrupt decline of the species' with its contraction of distribution, within the context of some caveats. Unfortunately, until relatively recently, population numbers were not regularly collected, meaning that available estimates are irregularly spaced, with large gaps for certain periods and multiple estimates for others. Additionally, many early studies, and particularly papers that only review the species in the context of other threatened primates (e.g. Tan 1985, Wang and Quan 1986), fail to acknowledge the source of the reported population estimates, or report the methods used to derive them, making their accuracy unknown. Indeed, even for those studies which do detail such methods, most neglect to outline the research effort involved, and several are not explicit

Table 2.2 Records of Hainan gibbon last occurrence locations and dates across Hainan by province (with associated references).

County	Last occurrence date	Last known locality	Reference(s)
Baisha	still extant		This study; BNNR Management Office (pers. comm., January 2014)
Baoting	1983	Diaoluoshan	Zhou et al. (2005)
Changjiang	still extant		This study; BNNR Management Office (pers. comm., January 2014)
Chengmai	1964	Chengmai	Zhou et al. (2005)
Danzhou	1950	Danzhou	Zhou et al. (2005)
Ding'an	1878		Wen (2009)
Dongfang	1978	Dongfang	Zhou et al. (2005)
Ledong	1983	Jianfengling	Zhou et al. (2005)
Lingao	1892		Wen (2009)
Lingshui	1983	Diaoluoshan	Zhou et al. (2005)
Qionghai	1964	Qionghai	Zhou et al. (2005)
Qiongshan (Haikou)	1917		Wen (2009)
Qiongzhong	1995	Limushan	Zhou et al. (2005)
Sanya	1964	Yaxian	Zhou et al. (2005)
Tunchang	1964	Tunchang	Zhou et al. (2005)
Wanning	1983	Diaoluoshan	Zhou et al. (2005)
Wenchang	1920		Wen (2009)
Wuzhishan	1983	Wuzhishan	Zhou et al. (2005)

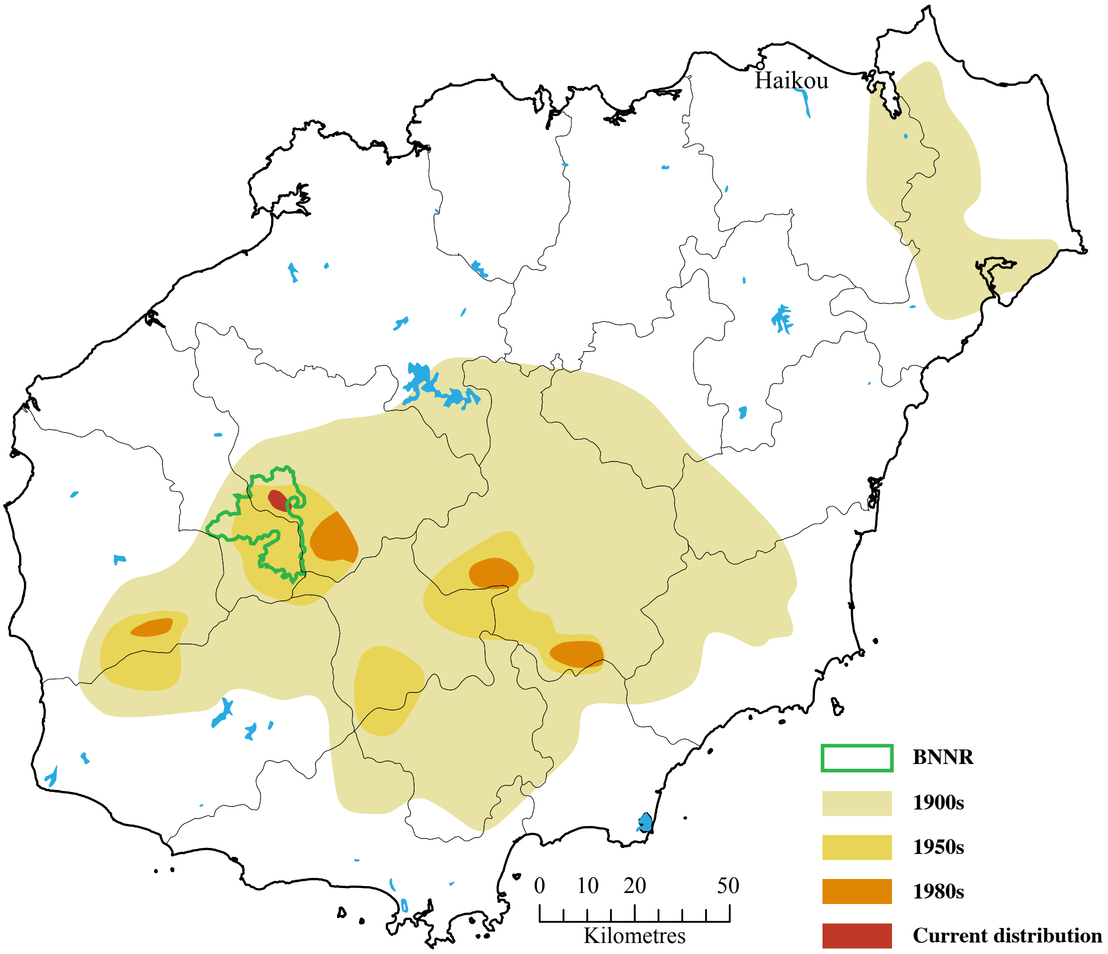


Figure 2.3 Purported historical distribution of Nomascus hainanus across Hainan by time period, showing range contraction from 1900 to current distribution; after Chan et al. (2005), Zhou et al. (2005), and this study.

about whether the estimate pertains only to Bawangling or to other sites on Hainan (an issue for estimates prior to 1989 when other populations still existed). This general lack of methodological detail and consistency impedes detailed statistical assessment of fine-scale population trends. However, by taking either the sole estimate or median value for years where a range of values are reported, it is possible to detect obvious patterns, specifically the precipitous decline in population size from the 1950s to the 1980s (Figure 2.4). Incorporating all estimates (including minimum and maximum estimates reported for a given year) for a shorter period (1978 onwards), it is clear that the species suffered a further decline in the 1990s. Although some in-country stakeholders consider the Hainan gibbon population to have risen continuously since the 2003 survey which detected 13 individuals (pers. obs., 2014 International Conservation Planning Workshop for the Hainan Gibbon, March 2014), it is clear from the compiled estimates that from 1989 onwards the population has fluctuated between around 15 and 25 individuals and has failed to grow beyond 25 individuals (Figure 2.5). This apparent oscillation may be due to a genuine fluctuation in population number, or may be a result of differential survey effort or detection success due to the technique or experience of researchers. Unfortunately, given the lack of disclosure of methods in most studies, it is not possible to be certain. Nevertheless, it does seem clear that the population has so far struggled to recover following its precipitous decline.

Causal factors: threatening processes behind the decline

Two main threats have been reported as the drivers of the decline of the Hainan gibbon: ongoing habitat loss and long-term targeted hunting (Chan et al. 2005). Liu et al. (1984) detailed the extirpation of the species from county to county across Hainan between the 1950s and early 1980s, pointing to two causes: i) a decline in the extent and condition of forest, recording a reduction from approximately 8,700 km^2 in the early 1950s to approximately 2,000 km^2 by 1983; and ii) intensive hunting, which continued despite low gibbon population size, reporting at least 40 gibbons being hunted within Bawangling and more than 200 forestry workers hunting gibbons in Jianfengling in the 1970s. These causes of decline were supported by Zhou et al. (2005), who linked what they identified as a marked acceleration in the decline of the species after the 1950s to the timber industry's policy of clear cutting, and the development of the rubber industry, under which many forests were replaced by plantations. The authors indicated that this extensive habitat clearance continued into the 1980s, coinciding with the development of Hainan and the accompanying increase in human pressure: “following the open-door policy in the Chinese economic arena; in particular after the formation of the Hainan Provincial Government in 1988, which was followed by numerous waves of human migrants to the island” (Zhou et al. 2005, p. 460). By 1999, the authors estimated that only 4% of primary forest remained on Hainan.

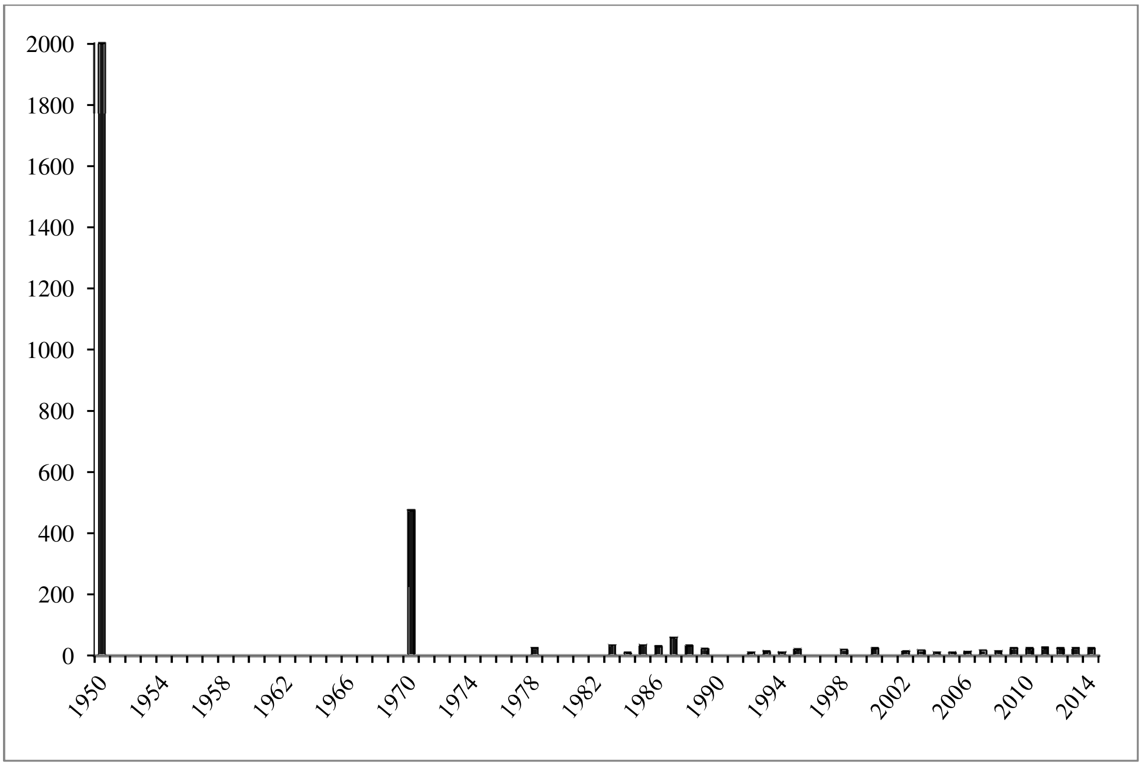


Figure 2.4 Graph of all Hainan gibbon population estimates available (medians where range available; sole estimate otherwise).

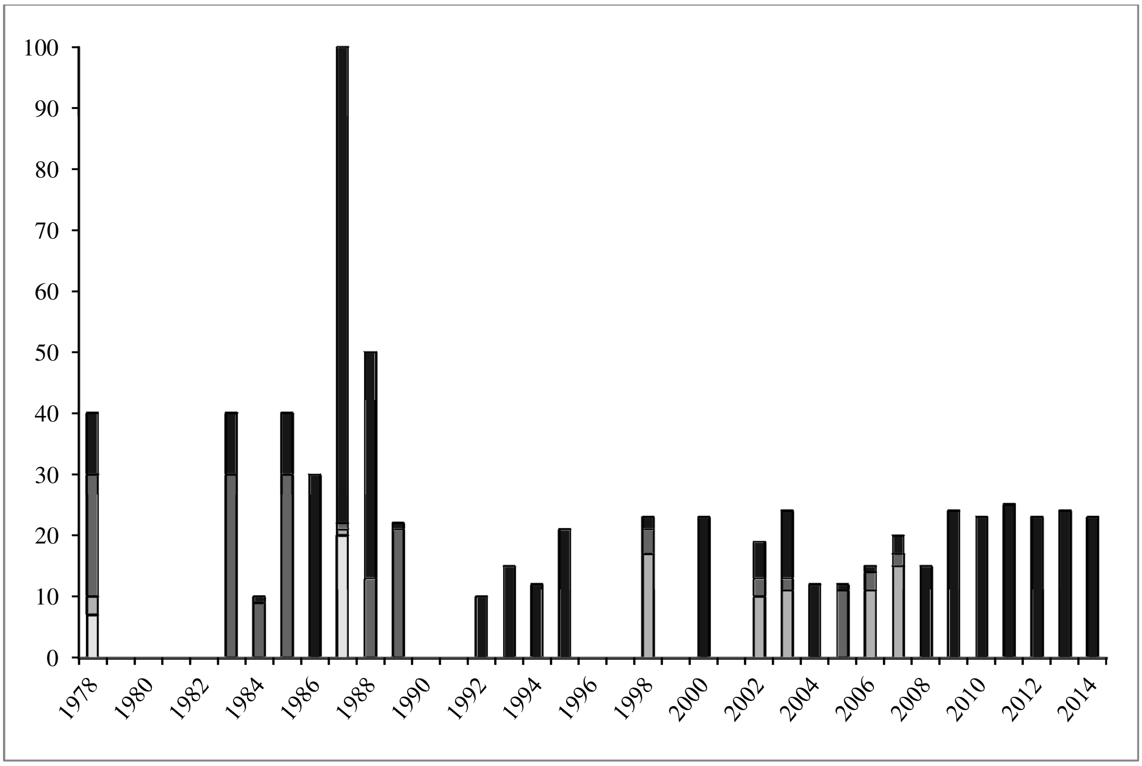


Figure 2.5 Graph of Hainan gibbon population estimates for 1978-2014 showing oscillation over last c. 30 years. Where a range of estimates was available: the minimum estimate for a year is indicated by lightest bar; the maximum by darkest; and intermediate estimates by graduations between.

Chan et al. (2005) and Zhou et al. (2005) each further detailed the role that hunting played in the species' decline, documenting evidence of numerous gibbon hunting bouts in Dongfang, Jianfengling, and Bawangling in the 1960s-1980s, which undoubtedly accelerated the disappearance of gibbon populations. Chan et al. (2005) indicated that the motivation for hunting was Traditional Chinese Medicine, with the local Miao and Li Hainanese minority groups reportedly hunting the species for its purportedly superior medicinal properties. Putative benefits are thought to be maximised when the whole body is made into a paste, known as 'Houzi Cream', believed to cure arthritis and accelerate general recovery (Zhou et al. 2005) . At least some parts of the Hainan gibbon's body have historically been used for additional, practical purposes, with Swinhoe (1870) reporting that the bones of the arm were used for chopsticks, and himself receiving such a pair of ulnae as a gift during his visit, which the giver (the secretary to the commodore at Nychow, South Hainan) planned to turn into chopsticks.

More recently, Zhang et al. (2010) provided new evidence of additional habitat loss, conducting the first detailed, statistical spatial analysis of the change in forest extent and condition (including fragmentation) across Hainan between 1991 and 2008. This study served to quantify the changes in gibbon habitat, namely the decline in core gibbon habitat (trees of >30 cm DBH comprising 70% of the canopy below 1300 m a.s.l.), that occurred during this time. This analysis showed that despite a ban on commercial logging on Hainan since 1994, vast tracts of prime gibbon habitat were lost, predominantly in low-elevation areas, from 1991 to 2008; in total, approximately 540 km^2 of gibbon habitat (and 1,462 km^2 of natural forest altogether). This loss of forest may account for the additional declines observed in gibbon population size during this period. The rapid, extensive clearing and continued degradation of natural forest across Hainan in the last 60 years, along with long-term intensive hunting of the species, are now generally regarded as responsible for the severe decline in the Hainan gibbon over the last century (Chan et al. 2005, Zhou et al. 2005, Zhang et al. 2010).

Conservation efforts to date

Due to the concern of Liu and colleagues over continued habitat loss threatening the Hainan gibbon's persistence, one of the last areas which the species then still occupied was protected in 1980: Bawangling Mountain was gazetted as Bawangling Nature Reserve to protect the remaining Hainan gibbon population and its habitat at the site. When raising the alarm about the critical state of the species, Liu et al. (1984) recommended a number of management strategies, including: public education to promote the species as an important piece of Chinese natural heritage; establishment of a reserve management agency for Bawangling; and formal government legislation to punish individuals caught hunting the species or destroying forest within the new reserve. These early conservation recommendations were met with some legislative support. In 1988 the reserve was upgraded to a National Nature Reserve and the Hainan gibbon was listed as Class I Nationally Protected Species under the Chinese Wildlife Protection Law (Government of the People's Republic of China, 1988), making it illegal to hunt the species. However over the next 10-15 years, enforcement of this legislation and commitment by the government to stop logging, even within the reserve area, were both apparently lacking (Chan et al. 2005, Zhou et al. 2005, Zhang et al. 2010), reflecting what was also an issue for gibbon conservation in other parts of China at this time (Bleisch and Chen 1990). By 1994 a ban on commercial logging of natural forest in Hainan was established, and in 2003 BNNR was expanded to its current size of almost 300 km^2 (Chan et al. 2005) and the species was formally recognised and listed as Critically Endangered by the IUCN (Geissmann and Bleisch 2008), affording it greater official protection.

The first Hainan gibbon conservation workshop was held in 2003, and by 2005 the first Conservation Action Plan was produced (Chan et al. 2005). This plan recommended management actions to address the recognised threats including: ongoing monitoring of the sole (BNNR) population; improved patrol effectiveness to minimise harmful human activities (hunting, logging, forest clearance); implementation of a publicity campaign to raise awareness of the Hainan gibbon; and re-forestation of degraded habitats in strategic locations with species valuable to gibbons. Additional recommendations focused on required research (such as improving understanding of the direct threats to gibbon survival, and locating any additional gibbons surviving in Hainan), and addressing impediments to effective management, namely building the capacity of the BNNR Management Office to conserve both the Hainan gibbon and the forest ecosystem as a whole. Many of these actions have subsequently been supported by congruent recommendations from various authors (Zhou et al. 2005, Lin et al. 2006a, Fellowes et al. 2008).

Lack of population growth

Despite past conservation efforts, which have focused on mitigating the acknowledged threats to the species, for the last 30 years the Hainan gibbon population has shown extremely limited growth, and appears to be constrained at around 25 individuals (Figure 2.5). As Fellowes et al. (2008, p. 7) reported: "Although the Hainan gibbon still breeds at natural birth intervals, the population has struggled to increase since the establishment of Bawangling Nature Reserve in 1980, after 27 years of forest protection by law". The reasons behind this apparent lack of recovery are not well understood. In the last 30 years of Hainan gibbon research, a number of potential constraining factors to gibbon population growth have been proposed, but these theories have generally lacked supporting evidence or have been based upon assumptions of patterns and apparent species characteristics, rather than direct demonstration of such trends or traits. For example, it has been argued that the limited amount of suitable available habitat (<15 km^2), in combination with the species' apparently large spatial requirements, is limiting the number of social groups and thus total gibbon population the reserve can support (Liu et al. 1989, Wu et al. 2004, Chan et al. 2005). However, the available estimates of the species' home range requirements are not supported by quantified, sound statistical analysis, making their accuracy unknown.

Low habitat quality has also been proposed as a threat to the species' recovery (Zhou et al. 2008b, Li et al. 2010), but again there has been no quantitative assessment of the extent to which degraded habitat influences or impacts upon the species. Chan et al. (2005) and Li et al. (2010) both argued, based on Liu et al.'s (1989) observation that nine of 12 offspring born between 1982 and 1989 were reportedly male, that the species may be exhibiting an imbalanced sex ratio, which could explain the lack of population growth through lack of available mates. As the sex of an individual cannot be reliably determined before sexual maturity (after which pelage colouration differs), confidence in claims of such an imbalance based solely on visual observations of immature gibbons is limited. Incest and inbreeding has also been blamed (Chan et al. 2005), but the authors provided no direct evidence to support such claims. As for many of the arguments about Hainan gibbon biology, the issue of assumptions versus defensible statistical patterns again applies. So, while there has been discussion about the probable causes behind the species' poor population growth, to date there has been little systematic investigation of the way in which gibbon biology and ecology, the current state of the habitat at BNNR, or ongoing human disturbance within the area, may actually be limiting the species' population growth. As Li et al. (2010, p. 525) concluded, "the reasons hindering the Hainan gibbon population rejuvenation are still not known".

Conclusion

From this synthesis of the available literature it is apparent that, despite over 30 years of research into the Hainan gibbon, there is still relatively little clarity about even the basic biology of this Critically Endangered species. There have been only a small number of direct studies to date which have revealed only basic insights into the species' spatial requirements, feeding ecology, reproductive biology, social structure, and broad population trends, with few conclusions supported by robust empirical data or comprehensive analysis. Much of this research has generally lacked a systematic approach, with studies often neglecting to adequately document their methodology or provide sufficient detail regarding their field methods, formal analyses and research effort. This lack of disclosure also complicates comparisons across studies, including investigation of fine-scale trends in population size over time, as it makes it impossible to control for variable effort. However, it is evident that the species suffered an abrupt and dramatic decline from the 1950s to the 1980s, with the main drivers of this decline being extensive habitat clearance and ongoing targeted poaching of the species. Since this initial population crash, the population has declined further and shown obvious instability, failing to recover beyond around 25 individuals despite a number of conservation measures being imposed to mitigate the main threatening processes. The reasons behind this lack of population recovery, and the intrinsic and extrinsic factors governing Hainan gibbon potential for population growth, are not well understood. A number of theories have been proposed, but again a lack of rigour in research approach and limited evidence for many of these claims confuses conclusion with assumption, and precludes confidence in such explanations.

Previous conservation recommendations for the species have inevitably been based upon information available to researchers and policy makers at the time, and as a result have, when viewed in a critical light, been founded upon conclusions with limited supporting evidence. Furthermore, most proposed conservation actions have focused on mitigating the immediate external causes of population decline, as is required (and in line with the ‘declining-population paradigm’), but have not attempted to address the issues associated with small population size (‘small-population paradigm’) or the intrinsic factors that will determine the species’ population growth (ecology, behaviour, genetic diversity) and long-term population viability. This is due to a deficit of direct, objective information regarding these factors. The need for additional research has been repeatedly acknowledged (Liu et al. 1984, Zhou and Zhang 2003, Wu et al. 2004, Zhou et al. 2008b), but as yet there has been only limited investigation of the species-specific intrinsic and extrinsic environmental factors which may influence population persistence and growth. Crucially, there has also been no critical assessment of the potential outcomes or likelihood of success of the conservation actions recommended to date, or other possible actions; a fundamental step in best-practice conservation planning (Akçakaya and Sjogren-Gulve 2000). As a result of the largely inadequate existing evidence-base, it is presently extremely challenging to derive meaningful conservation recommendations, or to make accurate predictions about the long-term likelihood of survival of the species. Additional rigorous and systematic investigation of the Hainan gibbon is imperative if the factors that may be restricting the growth, and thus recovery, of the last surviving population are to be understood, and appropriate, urgently needed steps to effectively manage the population are to be identified and implemented to prevent the extinction of the species.

Chapter 3. Quantifying the spatial home range requirements of the Hainan gibbon

Introduction

The social groups of virtually all primate species tend to confine their movement to a regular, defined area or 'home range' (Burt 1943) within their habitat to ensure they can reliably obtain the resources required to persist, mate and produce offspring with minimal energetic output (Mitani and Rodman 1979, Harvey and Clutton-Brock 1981). As a result of their specialised, highly efficient form of locomotion, brachiation, gibbons can surmount the energy and time costs of travel which constrain animal movement. Therefore, gibbons are able to range over large areas relative to other similar-sized mammals (Marshall et al. 2009). The Hainan gibbon is reported to exhibit the largest home range of any gibbon species (Chan et al. 2005, Li et al. 2010), with estimates ranging from 2 km^2 to nearly 10 km^2 (Liu et al. 1989, Liu and Tan 1990, Liu et al. 1995, Zhou et al. 2008a, Zhou et al. 2008b, Li et al. 2010). Indeed, Liu et al. (1995) argued that the Hainan gibbon's home range is tenfold larger than that of the Yunnan black crested gibbon (*Nomascus concolor*), reported to have a home range of between 0.5-2 km^2 (Lan 1989, Jiang et al. 1999, Fan and Jiang 2008a). Even the most closely related species, the Cao Vit gibbon (*N. nasutus*) has a mean home range of 1.3 km^2 (Fan et al. 2010, Fei et al. 2012). By comparison, most non-crested *Hylobates* and *Hoolock* gibbons have an average home range of 0.2-0.4 km^2 (Chivers 1984, Gittins 1984, Leighton 1987), making the home range requirements of *N. concolor* and *N. nasutus* an order of magnitude larger than generally observed in gibbons, and the estimates reported for the Hainan gibbon particularly remarkable. Consequently, although *Nomascus* gibbons may have larger home range requirements than their non-crested counterparts (Chan et al. 2005), from a comparative perspective, a tenfold difference between the Hainan gibbon and other members of its genus may be unlikely.

The mechanisms behind this reportedly exceptional home range are not clear, but previous authors have pointed to suboptimal habitat quality as a probable cause. Most optimal lowland forest across Hainan was destroyed between the 1950s and the 1980s (Liu et al. 1984), and by the late 1980s the sole surviving population was restricted to around 15 km^2 of contiguous, high-elevation habitat within Bawangling National Nature Reserve (BNNR) (Liu et al. 1989). Preferred gibbon food tree availability is thought to be substantially reduced in such habitat, meaning gibbon groups must travel longer distances to obtain sufficient nutrients (Liu et al. 1989, Chan et al. 2005, Zhou et al. 2008b). Other explanations include home range expansion as a result of low population density with few adjacent groups to restrict ranges, or that the large home range actually constitutes the natural state for the species (Fellowes et al. 2008). The Hainan gibbon's large proposed home range has also been cited as both a possible cause and effect of other aspects of the Hainan gibbon's biology that are similarly considered anomalous in comparison to other gibbon species. Gibbons are generally thought to form monogamous groups of an adult pair and 1-2 offspring (Carpenter 1940). Jiang et al. (1999) argued that the purported polygyny of the Hainan gibbon, suggested by observation of more than one adult female within a social group (Liu et al. 1989, Zhou et al. 2008b), results from the species' large home range permitting acquisition of sufficient resources to support multiple females within one group. Observations of large Hainan gibbon group sizes, on average 5-6 individuals (Liu et al. 1984, Zhou et al. 2008a) but sometimes up to 11 individuals (Li et al. 2010), have also been rationalised through the species' purportedly large home range. Liu et al. (1989) reasoned that the apparently large home range requirements of each social group will limit the formation of new social groups in the 15 km^2 forest fragment, such that individuals must remain within their natal groups.

In principle, the home range of a Hainan gibbon social group will have direct implications for the viability of the species. As most gibbon species tolerate only a very small amount of home range overlap between social groups (Ellefson 1968, 1974, Gittins 1980, Kappeler 1984), the spatial requirements of a gibbon social group could, by limiting the number of social groups that can exist within the available space (Reichard and Sommer 1997), limit population growth where that population has finite available habitat. Available habitat is extremely restricted for the Hainan gibbon, and the apparently anomalously large spatial requirements of the species have been proposed to explain the limited population growth observed in spite of protective measures being enacted since the 1980s. Liu et al. (1989) reported that by the late 1980s, available habitat within BNNR was probably close to limitation, with the then four groups estimated to collectively occupy a total of 12 km^2. Zhou et al. (2008b) also argued that a lack of vacant suitable habitat was preventing maturing gibbons from establishing their own territories, and Wu et al. (2004, p. 455) reasoned that the "…carrying capacity of the part of the reserve in which there are regular patrols is probably limiting the growth of the population".

Given the importance placed on the Hainan gibbon's spatial requirements in explaining the observed ecology of the species and its ostensible role in regulating the population's growth, accurate calculation of home range size is clearly vital for assessing the extent to which this factor may influence the capacity of the species to increase beyond its present size of around two dozen individuals. Unfortunately, interpretation of the few estimates of Hainan gibbon home range available is limited by largely inadequate reporting of the methodology and rigorousness of the approaches used to derive these estimates, with a general failure to disclose either the specific computational approach or survey effort employed. As a result, existing reports of Hainan gibbon spatial requirements do not allow us to critically evaluate the likelihood that the species really possesses such an exceptional home range, nor therefore the precise role that home range size may play in impeding the existing population's recovery. It is difficult to determine if the Hainan gibbon's purportedly large spatial requirements represent the inherent condition for the species, or are an artefact resulting from the species' extremely low population size and/or occurrence in potentially poor-quality habitat. Furthermore, the relationship between this and other aspects of the species' reported biology (including large group size and polygynous social structure) cannot be elucidated. This makes it impossible to adequately tailor management actions for the conservation of the species as it is not clear exactly which factors need addressing.

A more rigorous, systematic and methodologically-transparent investigation of the Hainan gibbon's home range requirements, using more advanced spatial analysis techniques, is a clear conservation priority for the species. I addressed this need by thoroughly re-evaluating the species' spatial requirements. I aimed to accurately quantify the home range of the Hainan gibbon, as well as detect any plasticity in this spatial requirement between seasons, and determine the extent of home range overlap between the existing social groups. I also critically assessed the reliability and representativeness of home range estimates through a number of evaluation approaches. These new, more robust home range estimates allowed me to evaluate the species' spatial requirements as a potential constraint to recovery given the extent of currently available habitat at BNNR. This work therefore sheds new light on the nature of this key aspect of the species' biology, which has to date restricted our ability to make proactive conservation decisions.

Methods

Data collection

New field data on Hainan gibbon ranging behaviour within BNNR were collected for the three existing social groups during two extended field seasons ('dry' season, November 2010–February 2011; 'wet' season, June 2011–September 2011) to enable detection of any seasonality in home range size. Non-invasive, minimally disturbing data collection techniques were employed. Gibbons were located with assistance from a team of BNNR wardens using the gibbon's loud, elaborate morning 'songs', which start just after dawn (peak singing period: 06:00-07:00 am) and occur at decreasing regularity later into the morning and afternoon (Liu et al. 1984, Chan et al. 2005). Using a collection of seven elevated listening posts previously established by BNNR Management Staff, songs were used to locate the three social groups based on their most recent sighting, in a variation of the fixed point survey method (Brockelman and Ali 1987, Brockelman and Srikosamatara 1993). Listening posts were manned from before dawn (05:00 am or earlier) until at least 12:00 pm, and only abandoned if no songs were detected during this time.

Groups were tracked on foot, and a systematic sampling scheme was used to record ranging movements, whereby geographic locations (waypoints with coordinates, elevation, fix error) were logged manually every 15 minutes using a hand-held GPS (Garmin GPSMap 60CSx). This sampling frequency was adopted to balance the speed at which gibbons move through the steep, often treacherous terrain, with the desired resolution (and independence) of data, and has been found to be appropriate for canopy-dwelling primates (Davenport et al. 2008, De Luca et al. 2010). During tracking I also recorded simple observations of the species' behaviour using a scan sample approach (Altmann 1974) against an ethogram (see Appendix C) developed after preliminary observations in reference to Chivers (1977). The behaviour of all visible group members, each observed for 5 seconds within a 1 minute scan, and the predominant behaviour within the group were noted with the aid of Nikon Monarch 8x42 binoculars. Food items consumed during feeding behaviours were also recorded. These behavioural data are not discussed further here but indicated that behaviour observed during tracking was typical of gibbon daily activity patterns seen in other species (see Appendix D) and thus collected ranging data were representative of normal home range use.

Groups were tracked for as long as possible and a follow ended when a group was lost due to its ranging speed or unsafe terrain. Observations were also limited by cultural considerations, which often meant that follows concluded mid-afternoon (between 13:30-15:00). This temporal bias is undesirable but any effect is likely to be negligible as many gibbon species settle at sleeping sites from early afternoon; *Hylobates lar* usually enter their sleeping trees at around 15:00 (but sometimes as early as 12:58pm) (Reichard 1998), and *N. concolor* at 17:00 (but sometimes as early as 15:00) (Fan and Jiang 2008b). Overall travel distance does not significantly differ between morning and afternoon tracking sessions for *Hylobates albibarbis* (Susan Cheyne pers. comm., July 2012), so there is little reason to expect that ranging data from only morning or afternoon tracking would misrepresent the ranging behaviour of the Hainan gibbon.

I attempted to track each social group for five consecutive days, and to intersperse the tracking of the social groups, but adverse weather and logistical issues occasionally prevented this sampling framework. The home range estimates reported in this study are defined for the sampling period and intensity as described here. More than 75 hours of observations of ranging behaviour were collected over 35 contact days, from a total of 93 field days across both field seasons. Observation, by necessity, focused on habituated Group 'B', as observation of unhabituated social groups 'A' and 'C' proved problematic due to the higher sensitivity of these groups and their tendency to move at speed to avoid being tracked. This is clear from the encounter success rates and locations collected for each group; only observation of Group B produced substantial data in both field seasons (Table 3.1). In total, an average encounter success rate of 41% yielded a dataset of 248 locations for the species. The three groups occupied distinct areas of the BNNR landscape during the course of the study, as can be seen from the final distribution of the group locations collected (Figure 3.1).

Table 3.1 Distribution of observations (effort and encounters) of Hainan gibbon social groups during the study by season ([*]represents success rate for each group, calculated by dividing the number of days yielding direct observations of the group by the number of field days dedicated to that group; [**]represents overall average success rate across all social groups).

Social group	No. of locations (*n*)	No. of field days	No. 'follow' (direct observation) days	Encounter success rate[*]	Hours of observation time
A -dry	6	12	3	25%	00:49:43
A -wet	4	10	2	20%	00:19:41
A	**10**	**22**	**5**	**23%**	**01:09:24**
B -dry	106	35	12	34%	31:46:44
B -wet	102	26	12	46%	31:49:31
B	**208**	**61**	**24**	**40%**	**63:36:15**
C (wet season only)	**30**	**10**	**6**	**60%**	**10:48:20**
TOTAL	**248**	**93**	**35**	**41%[**]**	**75:33:59**

Data analysis

Home range estimation

Numerous computational approaches are available to estimate home range, each with relative strengths and limitations (see reviews by Van Winkle 1975, Worton 1987), but there is presently no consensus regarding a ‘best’ estimation method (Walter et al. 2011, Downs et al. 2012). As estimates can vary with method (Harris et al. 1990, Grueter et al. 2009b), different approaches suit different underlying ranging distributions (e.g. clustered versus dispersed) (Getz and Wilmers 2004, Getz et al. 2007, Lichti and Swihart 2011) and will reveal different information about an animal’s space use (Kie et al. 2010), it is important to evaluate a species’ home range using multiple estimation methods. This approach is now widely-used (e.g. Huck et al. 2008, Moland et al. 2011, Pebsworth et al. 2012). I computed multiple metrics of home range to determine whether the estimates were robust to different analysis techniques and thus assess their reliability. Home range estimates were calculated for each existing Hainan gibbon social group, along with seasonal estimates for Group B, using each of the following methods.

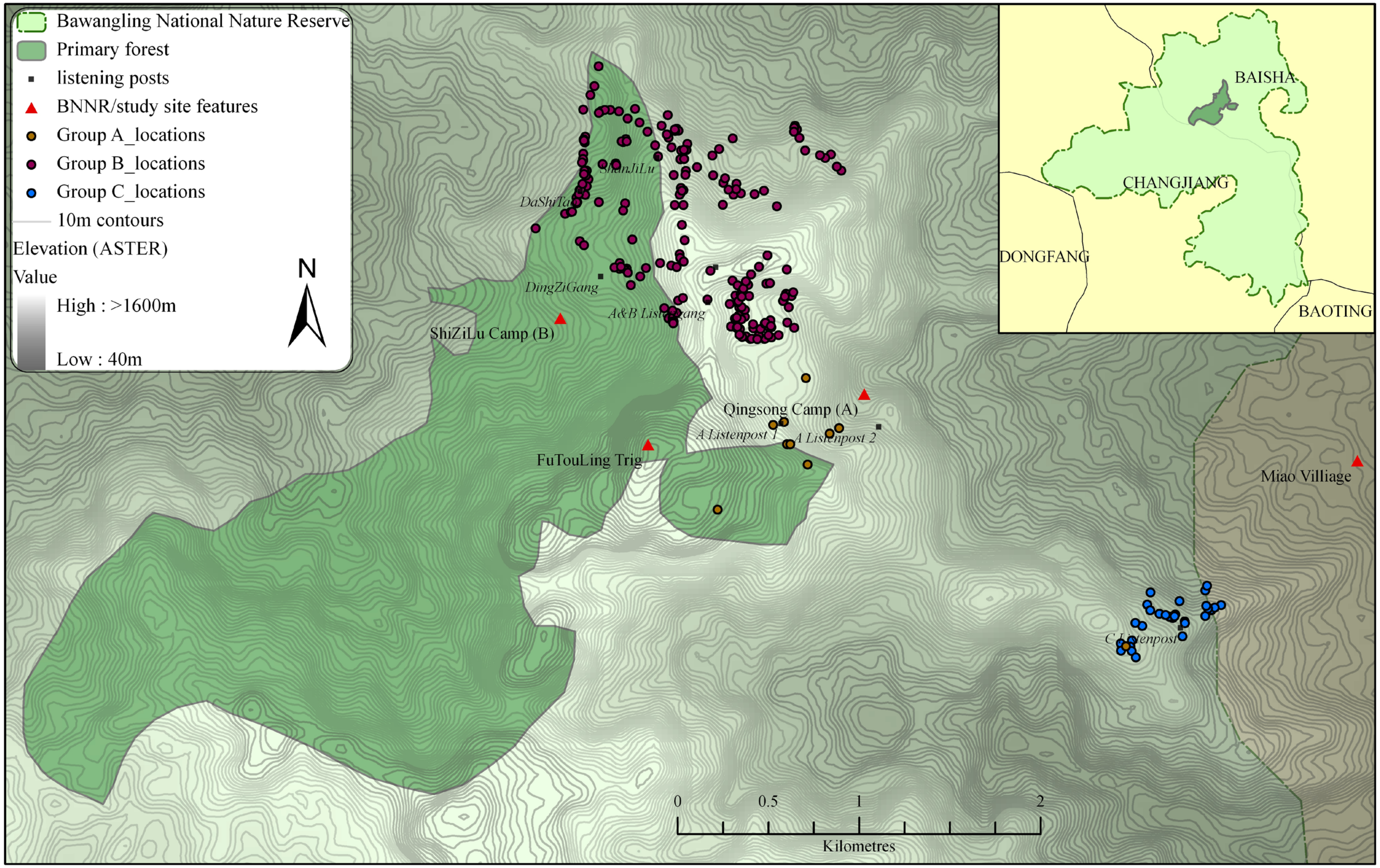


Figure 3.1 Location of Hainan gibbon social groups within Bawangling National Nature Reserve (BNNR), showing: ranging location datasets collected for each group; relative locations of groups; and key landscape features including study listening posts and primary forest area. Location of BNNR across two counties (Baisha, Changjiang) also shown.

1. Minimum Convex Polygon (MCP)

An MCP is constructed by connecting the outermost geographic locations of the dataset to form the smallest possible convex polygon (boundary) around all locations (Mohr 1947). This is the most basic representation of home range, but has been widely criticised due to several drawbacks including: correlation of estimates with sample size; assumption of uniform space use; inclusion of areas not visited by individuals within home range estimate; poor fit to non-convex home ranges; and no information about within-range variation in intensity of use (Burgman and Fox 2003, Börger et al. 2006, Getz et al. 2007, Kie et al. 2010). However, the MCP method allows for rapid home range assessment and is a widely-used technique, thus facilitating comparison with estimates of other species' home ranges. Indeed, although the methods used to calculate previous (large) estimates of Hainan gibbon home range are inadequately described, most appear to have been derived from MCP analysis. MCP estimates were calculated using Hawth's Analysis Tools V.3.27 (Beyer 2004) within ArcMap V.10.0 (ESRI 1999-2010), and incorporate all locations (100% of data).

2. Kernel Density Estimation (KDE)

KDE uses a non-parametric probability density function (or 'kernel') fitted over the entire dataset to smooth the data and estimate a continuous, two-dimensional probability distribution of space utilisation with contours (isopleths) that correspond to the amount of time that animals spend in different areas (Worton 1989). KDE can handle more complex location distribution patterns, allow for multiple centres of activity within the home range, and provide less biased estimates (Worton 1989, Seaman and Powell 1996, Swihart and Slade 1997, Lichti and Swihart 2011), making it a widely-used technique (e.g. Kolodzinski et al. 2010, Wartmann et al. 2010, Moland et al. 2011). A potential drawback to KDE is the assumption of serial and spatial independence of geographic locations, with early work suggesting non-independent 'autocorrelated' data may produce biased KDE estimates and underestimate home range (Swihart and Slade 1985a, b, 1997). However, more recent studies have indicated that autocorrelation may be less important than previously thought. De Solla et al. (1999) demonstrated that accurate KDE estimates do not require independent data points, and home range may be better represented by autocorrelated observations. Furthermore, autocorrelation may be an intrinsic property of home range (Valcu and Kempenaers 2010), and subsampling data to remove autocorrelation can remove the biological signal of interest (Blundell et al. 2001, Fortin and Dale 2005), which can lead to less precise estimates (Dray et al. 2010). For this reason, despite significant autocorrelation within the dataset (Schoener indices <1.6 or >2.4, and Swihart and Slade indices: >0.6; see Appendix E), no subsampling was performed prior to KDE estimation.

The choice of kernel smoothing factor or bandwidth (‘*h*’) will determine the shape of the utilisation distribution; larger bandwidths provide greater data-smoothing, whereas smaller bandwidths permit finer spatial resolution. Different bandwidth estimators are available, but there is little consensus regarding optimal methods (Seaman and Powell 1996, Kernohan et al. 2001, Gitzen and Millspaugh 2003, Gitzen et al. 2006). I used a fixed-bandwidth KDE approach (bandwidth remains constant throughout calculation) as this is less likely to overestimate home range (Seaman and Powell 1996), and adopted two widely used bandwidth estimators: least-squares cross-validation (LSCV) (Rudemo 1982, Bowman 1984), and PLUGIN (Wand and Jones 1994). Neither h-LSCV nor h-PLUGIN assume any underlying distribution of locations, but they appear to perform differently with different location distributions; h-LSCV is reportedly better at identifying tightly clustered data including areas of intense use, and h-PLUGIN is more appropriate for more dispersed data, where a species forages widely across much of its home range (Gitzen et al. 2006). KDE h-LSCV and KDE h-PLUGIN home ranges were calculated using the Geospatial Modelling Environment V.0.7.1.0 (Beyer 2012) to allow examination of the relative performance of each and thus the most appropriate KDE for the Hainan gibbon dataset, given the species’ ecology and observed location distribution. I report the KDE 90% isopleths (90% probability calculated using 100% of locations), as these have been found to reduce sample size bias and provide accurate estimates even with relatively few data (Börger et al. 2006).

3. Local Convex Hull (LoCoH)

The LoCoH method constructs convex hulls around each location and iteratively joins these hulls from smallest to largest into isopleths of space use, with each isopleth containing the corresponding percentage of points (e.g. 10% isopleth contains 10% of points), and smaller hulls corresponding to more heavily used regions (Getz and Wilmers 2004, Getz et al. 2007). LoCoH estimates can identify complex space use patterns, including concave boundaries and interior holes within a utilisation distribution, and minimise the inclusion of areas that occur outside true home range boundaries. They therefore perform better (particularly compared to KDE) at estimating home ranges where an animal’s landscape includes 'sharp' features including natural or imposed barriers to movement (e.g. lakes, fences, steep terrain, cleared forest) (Huck et al. 2008, Lichti and Swihart 2011). This is appropriate for the Hainan gibbon as there are known movement barriers within BNNR (cleared areas, plantations) (Chan et al. 2005), and as the species is reported to prefer vegetation between 800-1,200 m (Liu and Tan 1990), meaning that sharp boundaries, irregular shapes and interior holes are likely to occur in the home range.

I used the two available forms: fixed-k LoCoH (uses a fixed number of nearest neighbours (k-1) to a root point to construct hulls); and adaptive (a) LoCoH (number of points adapted by specifying the distance measure, ‘*a*’, with the sum of point distances from a root point $\leq a$

selecting the maximum number of nearest neighbours to construct hulls). To determine the optimal value of '*k*', I used the square root of the location (waypoint) dataset sample sizes for each group as an initial value, and then investigated the effect of varying *k* (above and below this value) upon the estimates generated. For '*a*' the initial values were set to the maximum distance between any two points within each group location dataset (calculated within ArcMap V.10.0, ESRI 1999-2010). The optimal values of *k* and *a* were identified as those that did not produce a further large 'jump' in home range size after an initial rapid increase, as per the minimum spurious hole covering (MSHC) rule outlined by Getz and Wilmers (2004). All LoCoH estimates were computed in R V.2.15.1 (R-Core-Team 2012) using the "adehabitat" package (Calenge 2006), and I report the 100% isopleths (containing 100% of locations) as smaller isopleths can omit areas known to be part of an animal's range (Getz et al. 2007).

4. Brownian Bridge Movement Model (BBMM)

The BBMM method incorporates an animal's movement trajectory when estimating home range by modelling an expected path using the 'Brownian bridge' movement model, which assumes animals move according to a 'random walk' between observed locations (Horne et al. 2007). Brownian bridges, which estimate the probability that the animal's trajectory has passed through any point of the study area, are placed over different sections of the observed trajectory and then summed over the entire area to produce a probability distribution of use, essentially smoothing the observed movement path rather than the entire location distribution as in KDE. Very few studies have employed the BBMM method to date (but see Huck et al. 2008), but theoretically this approach may provide more accurate estimates of home range as it makes more conservative assumptions about the use of space between recorded locations, and is less likely to include areas that are bound within recorded locations but not actually used. It is also not constrained by issues of location data independence, as it assumes that location data are autocorrelated and incorporates this into the model (Horne et al. 2007).

Two smoothing parameters are used in BBMM computation to incorporate uncertainty in the movement trajectory: $\sigma1$, which is related to the speed of the animal and describes how far from a line that joins two locations an animal can travel during one time step; and $\sigma2$, which is related to the imprecision of the locations recorded. I set $\sigma2$ to equal the estimated accuracy of the recorded locations (based upon the inherent locational accuracy of the GPS device and the average location fix error observed during data collection), and estimated $\sigma1$ using the maximum log-likelihood algorithm proposed by Horne et al. (2007), which relies upon $\sigma2$. The BBMM estimation approach was only adopted to assess Group B's home range, including seasonal ranges, as this was the only group for which it proved possible to collect successive locations and thus substantial movement data. BBMM home ranges were calculated in R V.2.15.1 (R-Core-Team 2012), using the "adehabitat" package (Calenge 2006). I report the 50% BBMM isopleths as these were the greatest probability isopleths to produce informative results (higher probability isopleths produced highly irregular polygons that extended far beyond the areas in which the group was ever observed including outside the BNNR boundary).

For all KDE, LoCoH and BBMM estimates, in addition to the specified % isopleth reported as home range, additional isopleths, inflated or deflated from this isopleth by 5-10% as appropriate for each estimation method, were also generated. These isopleths were produced to provide a simple representation of the sensitivity of each estimate and to permit future comparison with other studies employing such isopleths (e.g. the commonly used but less reliable 95% isopleth for KDE; Börger et al. 2006), as required. These supplementary isopleths are not discussed further but can be seen in the figures depicting home range spatial extents.

Seasonal and inter-group overlaps

To comprehensively assess the species' home range requirements, I investigated not only seasonal variation in home range extent, but also the overlap between seasonal ranges, to detect any partitioning of the yearly home range by season. Using the seasonal home range extents derived for Group B, for each estimation method I determined the area of overlap between wet and dry seasons and compared this to the larger of the two seasonal estimates, and the yearly estimate (of relevant estimate form). These figures indicated the proportion of the yearly and each seasonal home range utilised by the group in both seasons.

While only limited data were obtained for Groups A and C, given the importance of the assumption that neighbouring gibbon groups tolerate only modest home range overlap to the mechanism of a large home range potentially limiting population growth, it was important to quantify the extent of overlap between the group ranges. I determined the area of home range overlap between the groups as indicated by each of the different estimate forms and compared this to the home range of each group (relevant estimate form) to provide an indication of group home range overlap. For these analyses, spatial data manipulation and computation of overlap of home range extents were carried out within ArcMap V.10.0.

Assessment of estimate reliability

As the aim of this study was to derive a robust, accurate estimate of the Hainan gibbon's home range requirements, it was crucial to thoroughly assess the reliability of the estimates. I first assessed the variation in the estimates produced by the different estimation methods by computing the absolute difference in area (km^2) and relative difference (absolute difference in area divided by larger estimate). I also derived an additional metric I termed the 'minimum agreed area of use'. This constituted the minimum area covered by the spatial overlap of the different estimates, and therefore the spatial extent that the various estimates agreed that the group utilised. To determine this metric, it was necessary to use a selection of estimates (only one of each estimate form). Including multiple forms of a given estimate would have skewed the agreed overlap area towards the area reported by those estimates (which are more likely to be spatially concordant). The estimates employed for this calculation were the MCP, KDE-PLUGIN, a-LoCoH, and BBMM based upon a preliminary assessment of the performance of the multiple KDE and LoCoH estimates against the underlying location distribution. Estimate overlaps were computed within ArcMap V.10.0.

I further assessed the reliability of the home range estimates in the following three, more complex ways.

1. Incremental Area Analysis (IAA)

The sample size of a location dataset can alter a home range estimate, but there is no clear indication of the 'minimum' number of locations required to describe an animal's home range accurately (Harris et al. 1990, Girard et al. 2002, Boyle et al. 2009, Kolodzinski et al. 2010, Lichti and Swihart 2011). Given the relatively small size of the ranging datasets collected, a key step in assessing the reliability of the estimates was to evaluate the representativeness of underlying dataset. I conducted an Incremental Area Analysis (IAA) (Kenward and Hodder 1996) using ABODE (Laver 2005) within ArcMap V.10.0. This approach generates incrementally larger datasets through random selection (subsampling) of locations from a given dataset. Random selection was appropriate as, while locations were collected continuously during a follow, separate follows were temporally discrete, and therefore the data were 'discontinuous' over the entire sampling period (one year). MCPs were produced for the incrementally larger datasets to investigate the relationship between home range and sample size, and to investigate whether the home range estimate reached a plateau with the increasingly larger dataset collected.

To formally evaluate any plateau behaviour, I assessed the IAA curves produced against three regression models: a simple linear model and two asymptotic exponential models in R V.2.15.1 (R-Core-Team 2012). The asymptotic models used were a three-parameter exponential model ('SSasymp') and a two-parameter exponential model passing through the origin ('SSasympOrig'). The second-order Akaike Information Criterion (AICc; Hurvich and Tsai 1989), as appropriate for smaller sample sizes, was computed for each model using the "AICcmodavg" package (Mazerolle 2012) to assess the performance of the models and determine which provided the best model fit for the IAA curves. I tested for statistical distinction between models (ANOVA), and compared model AICc values to determine the AIC difference (i.e. ΔAIC; Akaike 1973, here ΔAICc) and ranked the models accordingly. A rule of $\Delta AIC>4$ was used to identify models that were a substantially better fit than the null model (Burnham and Anderson 2004). Model fit was also assessed by checking for overdispersion.

Residual deviance was computed and compared to the degrees of freedom, and the probability of observing this deviance by chance against the chi-squared distribution determined (Dalgaard 2008). It was clear from visual inspection of the IAA curves for Groups A and C that no plateau was reached, so this formal curve assessment was conducted for Group B data only.

2. Geographic concordance

I also measured the extent to which the different estimate forms reached spatial concordance regarding the area utilised by each group. I determined the degree of agreement between pairs of estimates by assessing the area of spatial overlap. This indicated the geographic concordance of estimates, not just any agreement in terms of home range size. I compared this area of overlap against the larger of the two estimates of home range to determine the relative percentage of overlap. I conducted these pair-wise comparisons within ArcMap V.10.0, for each group estimate and seasonal estimates for Group B. I expected greater spatial concordance between the Group B estimates than for Group A or Group C estimates due to relative sample sizes, and greater concordance between estimates generated for an individual group using methods with similar computational and/or theoretical approaches (e.g. LoCoH as a derived form of MCP; BBMM as a more explicit 'kernel' than KDE).

3. Performance of estimates against relevant landscape features

Elevation (along with aspect) can determine habitat characteristics (e.g. vegetation type, density, productivity) that will be fundamental to understanding gibbon group ranging. Within BNNR, areas above 1,200 metres elevation above sea level (m a.s.l.) are unlikely to be floristically suitable for gibbons (Liu and Tan 1990), and much of the area below 800 m is also unsuitable as most primary vegetation has been cleared or replaced by economic plantations, including pine and rubber (Chan et al. 2005, Zhang et al. 2010). It was therefore possible to assess the reliability of the estimates by investigating their ability to exclude areas from the home range which we would not expect the Hainan gibbon groups to utilise. This would also serve to substantiate or refute this reported elevation preference, and so provide insight into the drivers of Hainan gibbon ranging patterns.

To assess estimate performance I extracted elevation contours from a high-resolution (1-arc-second/30 metre) global Digital Elevation Model (DEM): the Advanced Spaceborne Thermal Emission and Reflection Radiometer Global DEM (ASTER GDEM V.2, NASA and METI 2011). I rasterised and resampled the DEM data (using a circular neighbourhood focal statistic with search radius of one cell) to smooth the data, as contours interpolated directly from raw DEM data can show artefacts produced as a result of DEM registration and seaming (e.g. gaps, self-intersecting contours, angular lines in flat areas) (Ozah and Kufoniyib 2008). I generated a 10 metre interval contour dataset, which I then compared to the elevations recorded by the handheld GPS for a subset of locations (12 key geographic locations used during fieldwork) to assess the accuracy of the generated contour dataset. The average difference (in metres) between the GPS-described elevations and the DEM-derived contour nearest the features was found to be minimal (see Appendix F), indicating the validity of adopting the contour dataset. Areas in BNNR at elevations above 1,200 m and below 800 m a.s.l. were then identified as expected holes within group home ranges, and the performance of each home range estimate was visually assessed against these areas for Group B estimates only (due to small samples for the other groups limiting the meaningfulness of such analysis). I expected that estimates from the more derived estimation techniques (e.g. LoCoH) would perform better in this regard and so provide a more accurate representation of the species' home range requirements. All spatial data manipulation, analysis and map generation was carried out in ArcMap V.10.0.

Results

Home range size

The different estimation techniques produced a range of estimates of home range area for the three social groups and for Group B's seasonal home ranges, which vary quite markedly. Group B's yearly home range was estimated at between 1.28-1.92 km^2 (Figure 3.2). The seasonal home ranges of this group appear to be slightly smaller, with dry season home range estimated between 0.72-1.38 km^2, and wet season home range between 0.66-2.27 km^2. For Group A, based upon the very small dataset, the home range was estimated at between 0.15-2.54 km^2 (Figure 3.3). Group C's home range was estimated to be much smaller, between 0.06-0.20 km^2 (Figure 3.4), however this represents only wet season data for this group.

The KDE h-LSCV approach generally produced the most generous estimates of home range size for all home ranges, and the BBMM approach also generated larger estimates for Group B. The LoCoH estimates (fixed or adaptive) were the most conservative for all group home ranges. The KDE h-PLUGIN and MCP estimates were intermediary, with one of these two estimates generally closest to the median of all estimates for each group and seasonal ranges (Table 3.2). The variation observed between estimates was relatively low for Group B, with the smallest and largest estimates differing by only 33% for this group's yearly estimates. Greater variation between estimates was apparent for the home ranges derived from the smaller datasets. The variation was most extreme for Group A, for which the fewest data were obtained, with a difference of almost 94% observed between the smallest and largest estimates. However, the variation observed for the Group C estimates and the Group B wet season estimates was roughly the same (just over 70% difference), suggesting that estimate variation with estimation technique was not just influenced by sample size.

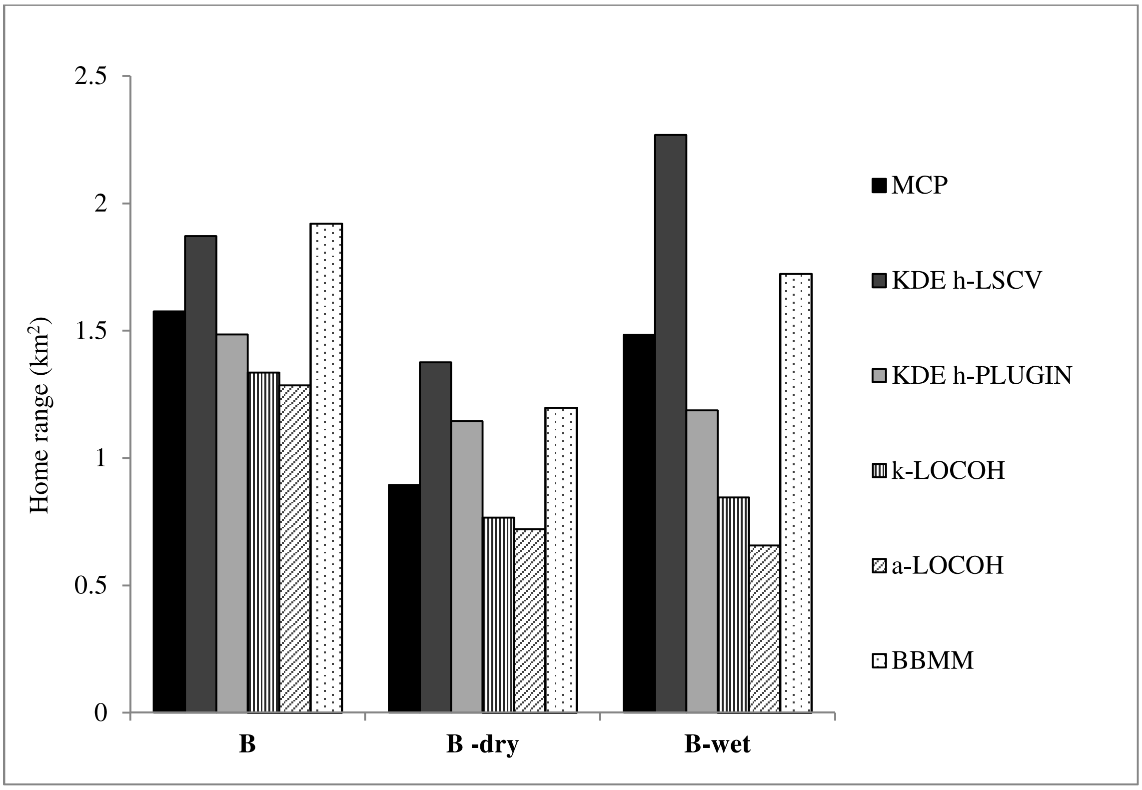


Figure 3.2 Estimates of Group B yearly, dry and wet season home ranges (km^2) by estimation method.

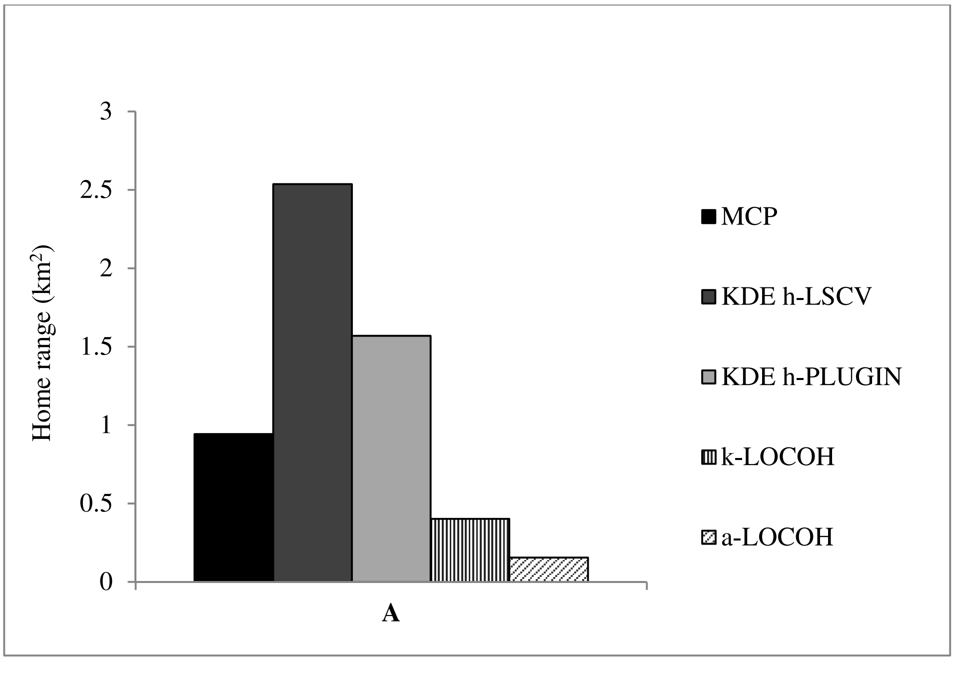


Figure 3.3 Estimates of Group A yearly home range (km^2) by estimation method.

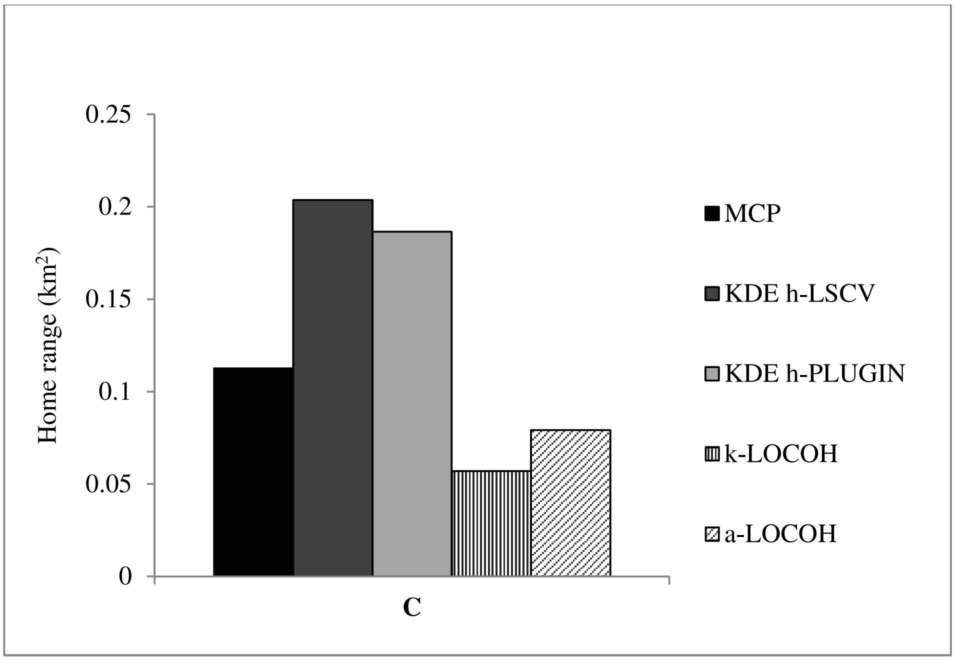
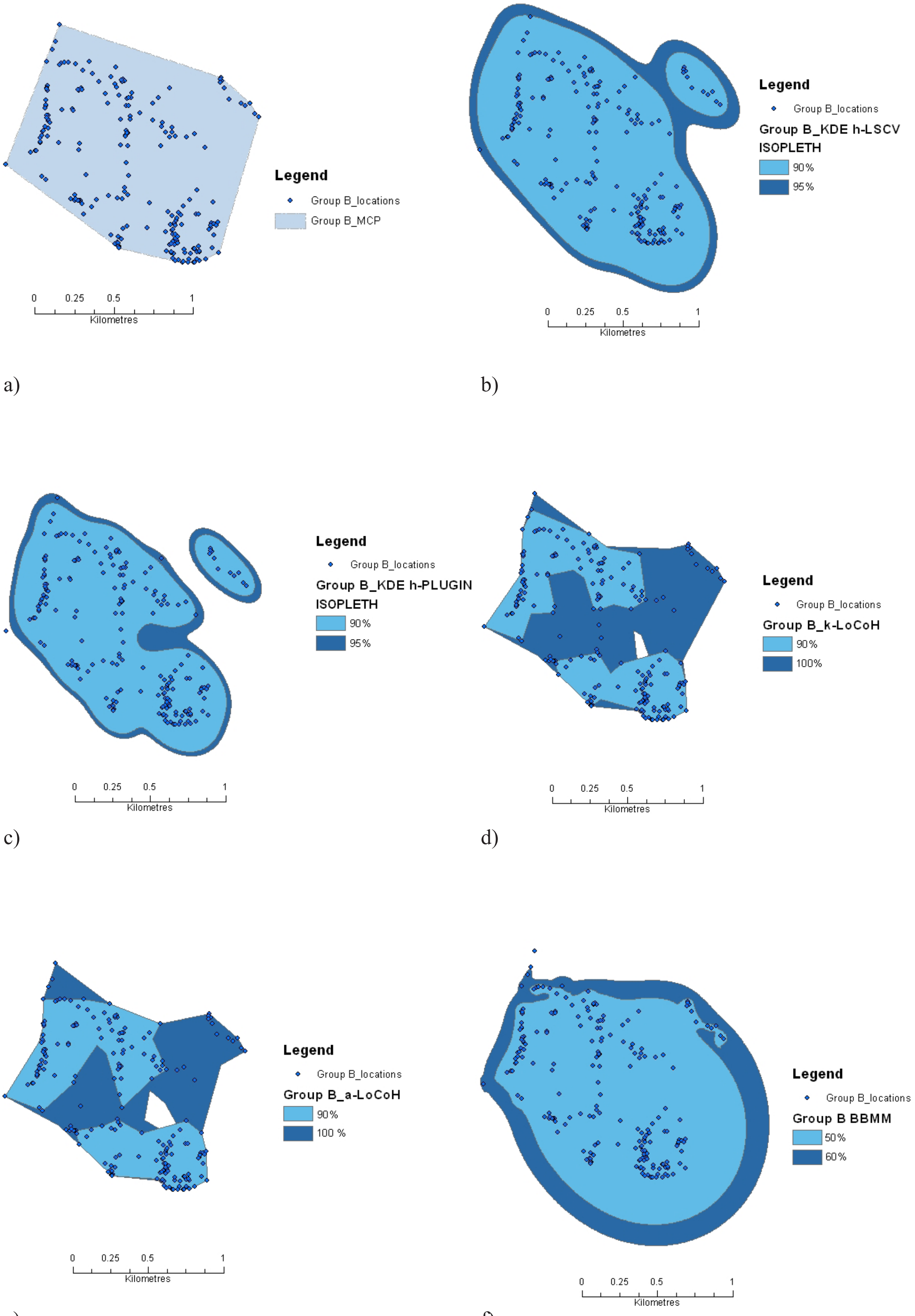


Figure 3.4 Estimates of Group C home range (km^2) by estimation method (corresponds to wet season only).

The minimum agreed area was more conservative than the smallest yearly and seasonal estimates of home range for Group B. The minimum area that all estimates indicated was within the group's yearly home range is around 1 km^2, and closer to 0.5 km^2 for the seasonal home ranges. It is clear that the different home range estimates are therefore making different assumptions about the use of space between (and outside) collected locations (Figures 3.5, 3.6, 3.7), but they agree that the group utilises at least this minimum area for their yearly and seasonal home ranges. The minimum agreed area for Group A was merely equivalent to the smallest estimate produced (a-LoCoH), and for Group C was just slightly larger than this group's smallest estimate (k-LoCoH). This indicates that the different estimates for these two groups varied substantially in terms of the area between and around geographic locations included within the respective group ranges (Figures 3.8, 3.9).

Table 3.2 Variation in home range estimates produced from different estimation methods for each social group (and seasonal home ranges for Group B). Metrics include: smallest and largest estimates; absolute difference in area between smallest and largest estimates; relative difference between smallest and largest estimates (absolute difference in area divided by larger estimate); median of the estimates for each home range estimated; home range estimate closest to this median value; and the 'minimum agreed area' of estimates (smallest area of spatial overlap of MCP, KDE-PLUGIN, a-LoCoH, and BBMM estimates).

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



a) b)

c) d)

e) f)

Figure 3.5 Spatial extent of Group B yearly home range as reported by a) MCP, b) KDE h-LSCV, c) KDE h-PLUGIN, d) k-LoCoH, e) a-LoCoH and f) BBMM estimation methods.

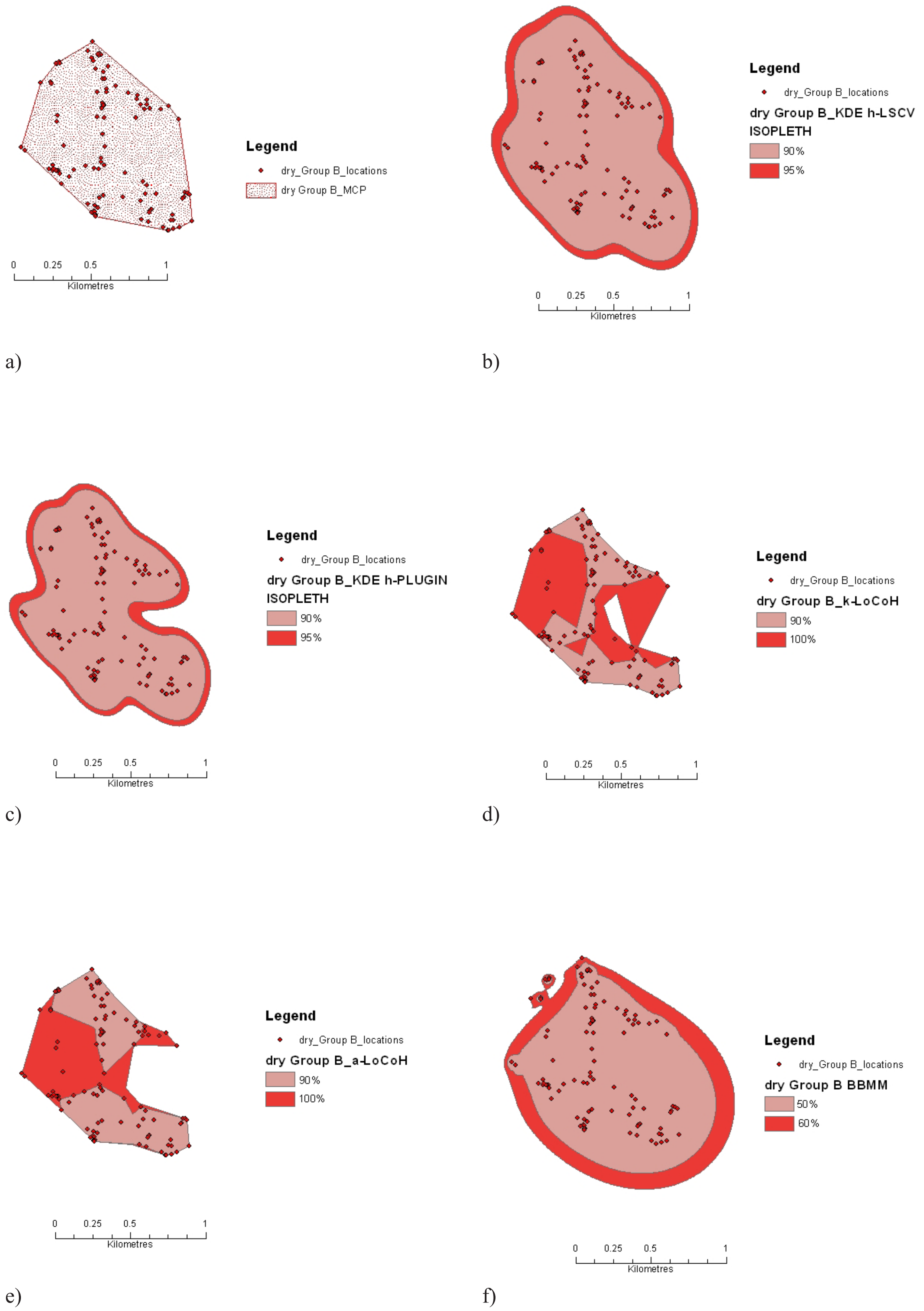


Figure 3.6 Spatial extent of Group B dry season home range as reported by a) MCP, b) KDE h-LSCV, c) KDE h-PLUGIN, d) k-LoCoH, e) a-LoCoH and f) BBMM estimation methods.

Figure 3.7 Spatial extent of Group B wet season home range as reported by a) MCP, b) KDE h-LSCV, c) KDE h-PLUGIN, d) k-LoCoH, e) a-LoCoH and f) BBMM estimation methods.

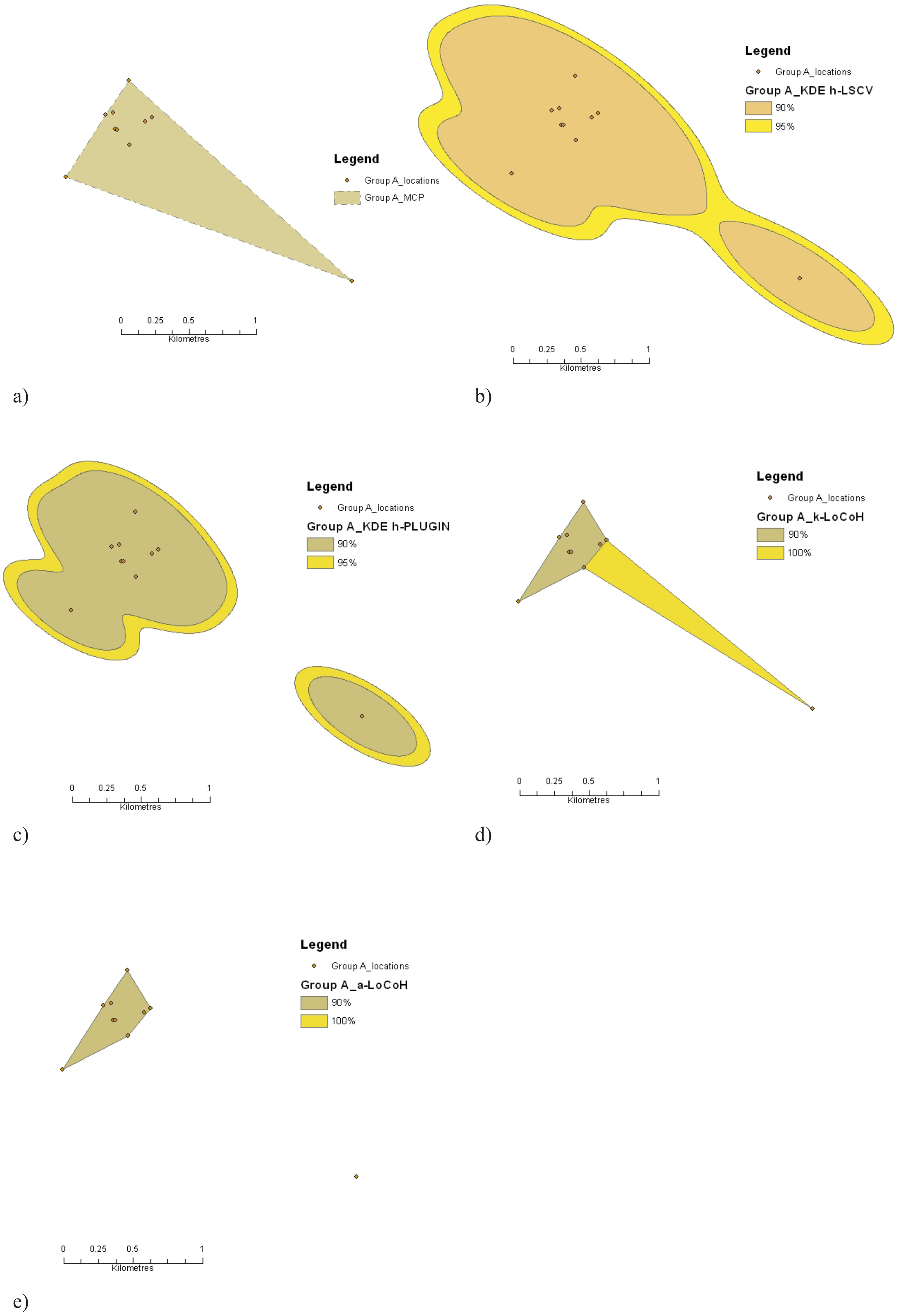


Figure 3.8 Spatial extent of Group A home range as reported by a) MCP, b) KDE h-LSCV, c) KDE h-PLUGIN, d) k-LoCoH, and e) a-LoCoH estimation methods.

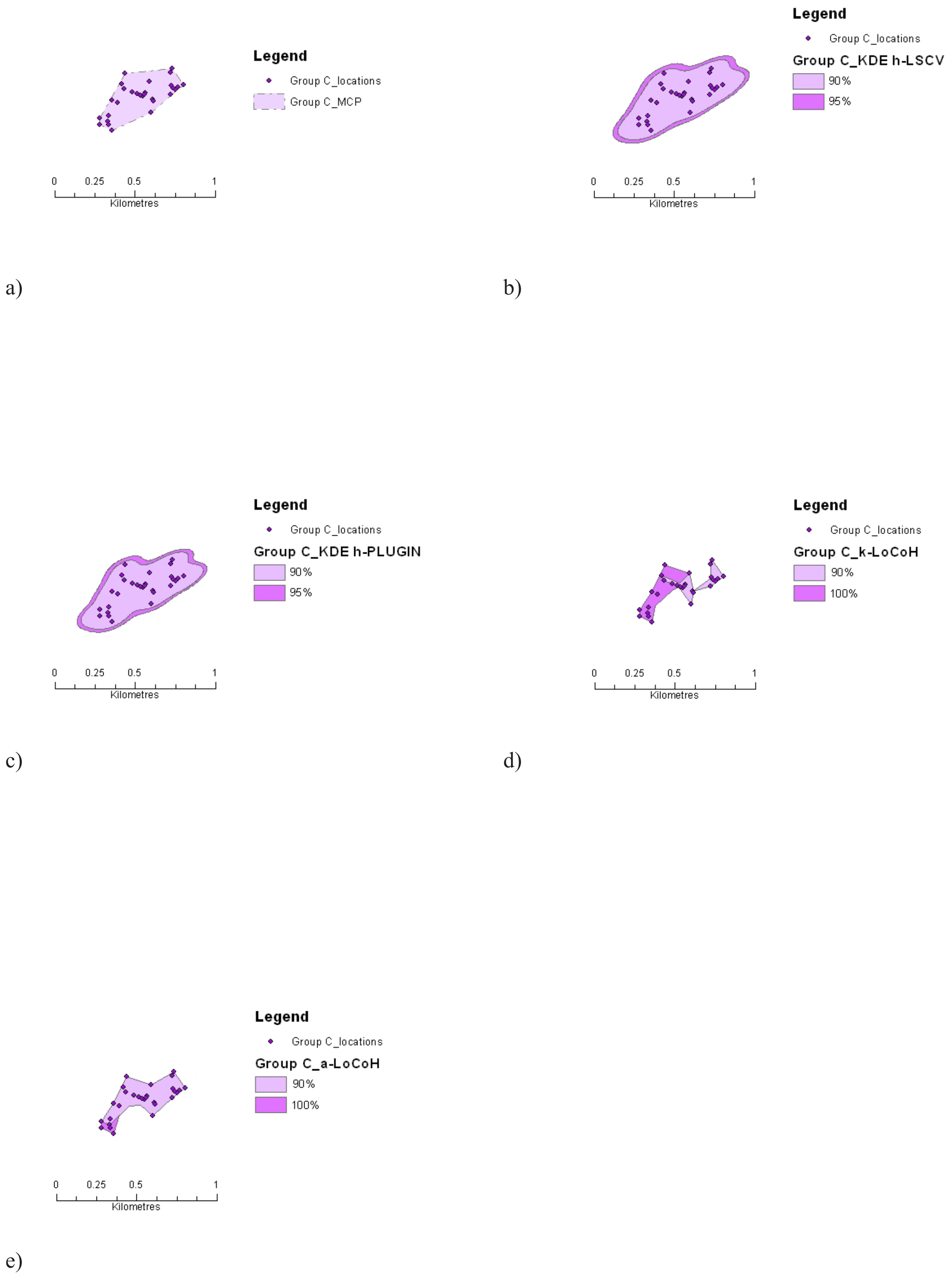


Figure 3.9 Spatial extent of Group C home range as reported by a) MCP, b) KDE h-LSCV, c) KDE h-PLUGIN, d) k-LoCoH, and e) a-LoCoH estimation methods.

Seasonal ranges and overlap (partitioning of yearly home range)

The seasonal estimates for Group B differ in both home range size and geographic location. Taking the median estimates for each season as a guide (Table 3.2), and considering the patterns for each estimate form (Figure 3.2), there is some evidence for a slightly larger home range in the wet season, with the MCP, KDE h-LSCV and BBMM estimates showing this most markedly. The home range polygons indicate that the group also utilises different areas of its yearly home range in each season (Figures 3.6, 3.7); however, this difference was only reported by the KDE h-PLUGIN and LoCoH estimates (both variants). This variation in the degree of seasonal home range partitioning being dependent upon estimation method was also seen in the amount of overlap between estimates for each seasonal home range. The degree of seasonal home range overlap indicated by the MCP, KDE h-LSCV and BBMM estimates was much greater (0.85-1.20 km^2 or 53-61% of the larger seasonal home range estimate; Table 3.3), than that reported by the KDE h-PLUGIN and both LoCoH estimates (0.17-0.57 km^2 or 24-48% of the larger seasonal home range estimate), which therefore suggest greater partitioning. Similarly, the proportion of the yearly home range that this seasonal overlap represented, corresponding to the area the group utilises all year, was reported as only 13.3-38.6% by the KDE h-PLUGIN and LoCoH estimates, but between 54-65% by the MCP, KDE h-LSCV and BBMM estimates. It is clear therefore that the conclusions we draw about the group's seasonal home ranges will depend upon which estimation approach we adopt. Taking a median value suggests that 0.71 km^2, or roughly 50% of the yearly home range, is used in both seasons.

Table 3.3 Group B seasonal home range overlap by estimation method. Overlap is quantified in terms of: area of overlap; relative overlap (calculated against the larger of the two seasonal estimates); and relative percent of the yearly home range area the overlap represents. Median overlap represents the median of all estimates of seasonal overlap.

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

Group home range overlap

Groups occasionally ranged in the same areas or were tracked to areas where another group had previously been observed, but the degree of quantified group overlap was dependent upon estimation method. Three of the five estimate forms indicated extremely little (<0.15%) or no overlap between the group home ranges for Groups A and B and Groups A and C (Table 3.4). The other two estimates (the KDE variants), which reported larger individual group ranges, described an area of overlap between 0.09-0.32 km^2 for Groups A and B, corresponding to 6-17% of an individual group's home range (depending upon the group). The overlap between Groups A and C was estimated to be much smaller (c.0.07 km^2), which could either be as little as 3% or as great as almost 43% depending upon the group home range estimate to which this area is compared. This large variation in estimated amount of overlap between groups is likely to result from the greater uncertainty in individual home range estimates for Groups A and C. Groups B and C were never observed in the same location, and therefore no home range overlap was expected or reported by any of the estimates.

Assessment of estimate reliability

Incremental Area Analysis

Visual inspection of the IAA curves indicated that the yearly and seasonal datasets collected for Group B were both representative, with the MCP home range estimates for this group plateauing as the number of locations used to construct the home range increased. Regression analysis confirmed the asymptotic nature of all three of these datasets (Figures 3.10, 3.11, 3.12). None of the regression models suffered from overdispersion (probability of observed residual deviance >0.995 for all models, data not shown). The linear and two asymptotic exponential models were all significantly different from each other (ANOVA, $P<0.001$; Table 3.5), and all terms of the complex three-parameter exponential models ('SSasymp') were significant for all three Group B IAA curves ($P<0.001$, parameter estimates each >2 S.E. difference), indicating model simplification was not justified and the three-parameter exponential model was appropriate. This model performed better at explaining the relationship between location number and estimated home range area for the yearly and wet season datasets based upon AICc rankings and relative differences (ΔAIC >15; Table 3.5). For the dry season dataset, the three-parameter model was only a marginally better fit than the two-parameter model (ΔAIC=2.56). The three-parameter exponential model also performed better than the simple linear model (ΔAIC >15) for all three datasets, indicating that the IAA curves are better described by either exponential model than a linear model, supporting the asymptotic nature of the IAA curves and representativeness of these datasets.

Table 3.4 Overlap between group home ranges by estimation method. Overlap is quantified in terms of area of overlap and relative overlap calculated against both the larger and smaller home range estimates for the groups compared.

Estimate	Groups A and B			Groups A and C		
	Area of overlap (km^2)	**Relative overlap (% of Group A home range, larger)**	**Relative overlap (% of Group B home range, smaller)**	**Area of overlap (km^2)**	**Relative overlap (% of Group A home range, larger)**	**Relative overlap (% of Group C home range, smaller)**
MCP	none	none	none	<0.0002	0.0%	0.2%
KDE-LSCV	0.32	12.7%	17.2%	0.08	3.3%	42.5%
KDE-PLUGIN	0.09	6.0%	8.5%	0.07	4.3%	35.5%
k-LoCoH	none	none	none	<0.0001	0.0%	0.1%
a-LoCoH	none	none	none	none	none	none

Table 3.5 ANOVA comparisons of three regression models assessed for Incremental Area Analysis curves of Group B yearly, dry and wet home range datasets, with AICc and ΔAICc values, and corresponding model rankings.

Dataset	**Model form**			**AIC_c**	**ΔAIC_c**	**Model Rank**
		lm	SSasymp			
B (year)	lm			-233.91	-197.99	3
	SSasymp	F=448.15 *P*<0.001		-431.91	0.00	**1**
	SSasympOrig	F=448.15 *P*<0.001	F=163.67 *P*<0.001	-312.19	-119.72	2
B -dry	lm			-209.89	-40.90	3
	SSasymp	F=213.75, *P*<0.001		-250.79	0.00	**1**
	SSasympOrig	F=213.75, *P*<0.001	F=4.70, *P*<0.05	-248.23	-2.56	2
B -wet	lm			-28.69	-275.34	3
	SSasymp	F=192.73, *P*<0.001		-304.04	0.00	**1**
	SSasympOrig	F=192.73, *P*<0.001	F=29.50, *P*<0.001	-279.66	-24.38	2

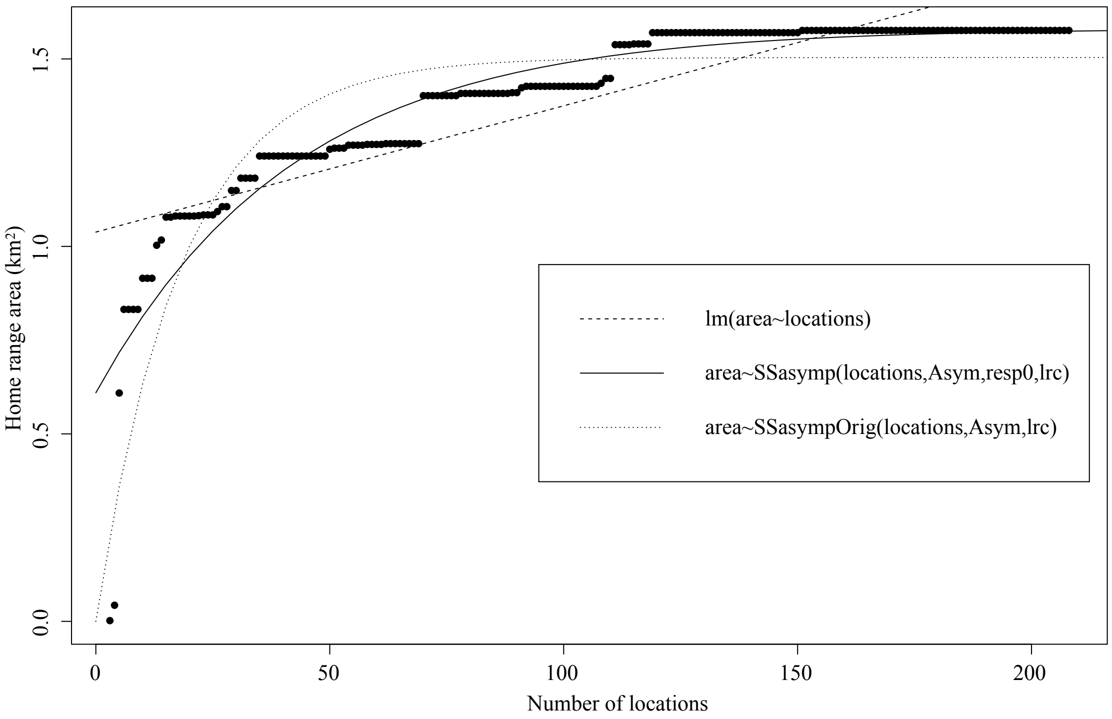


Figure 3.10 Performance of Incremental Area Analysis curves (solid black circles) generated for Group B yearly home range dataset (locations sampled randomly from each dataset to construct incrementally larger home ranges) against three regression models: a simple linear model (lm), and two asymptotic exponential regression models; three-parameter model ('SSasymp') and two-parameter model passing through the origin ('SSasympOrig). The two-parameter asymptotic exponential model was chosen to confirm the sample size value at which each Group B home range estimate stabilised.

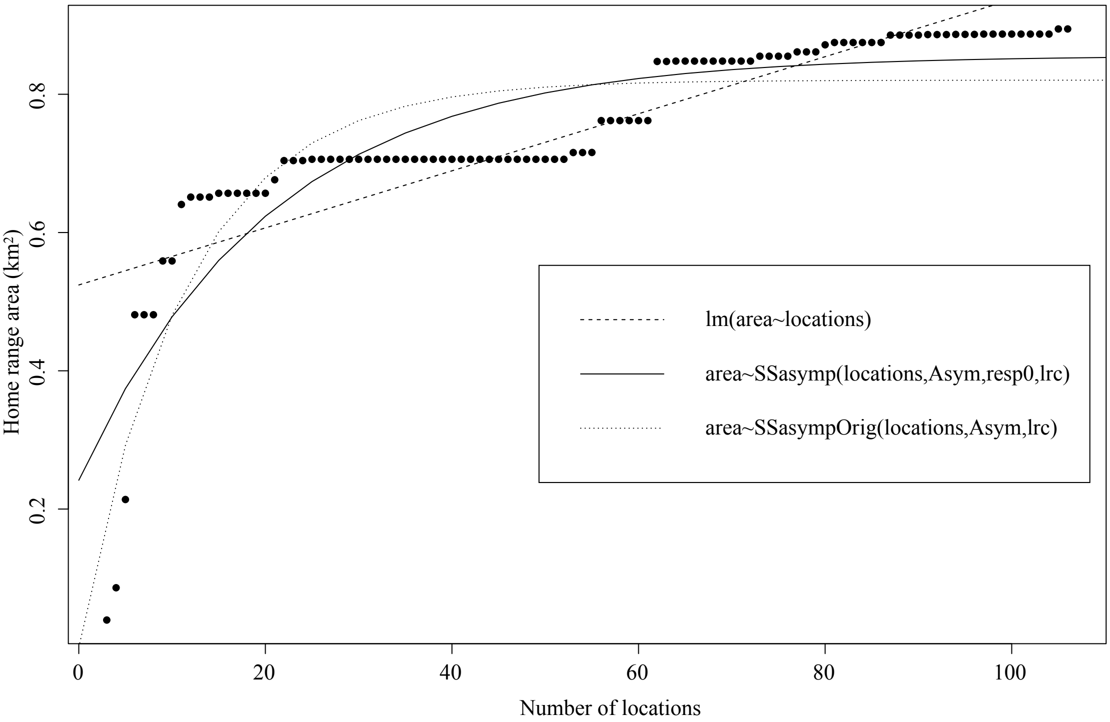


Figure 3.11 Performance of Incremental Area Analysis curves (solid black circles) generated for Group B dry season home range dataset against three regression models -caption as per Figure 3.10.

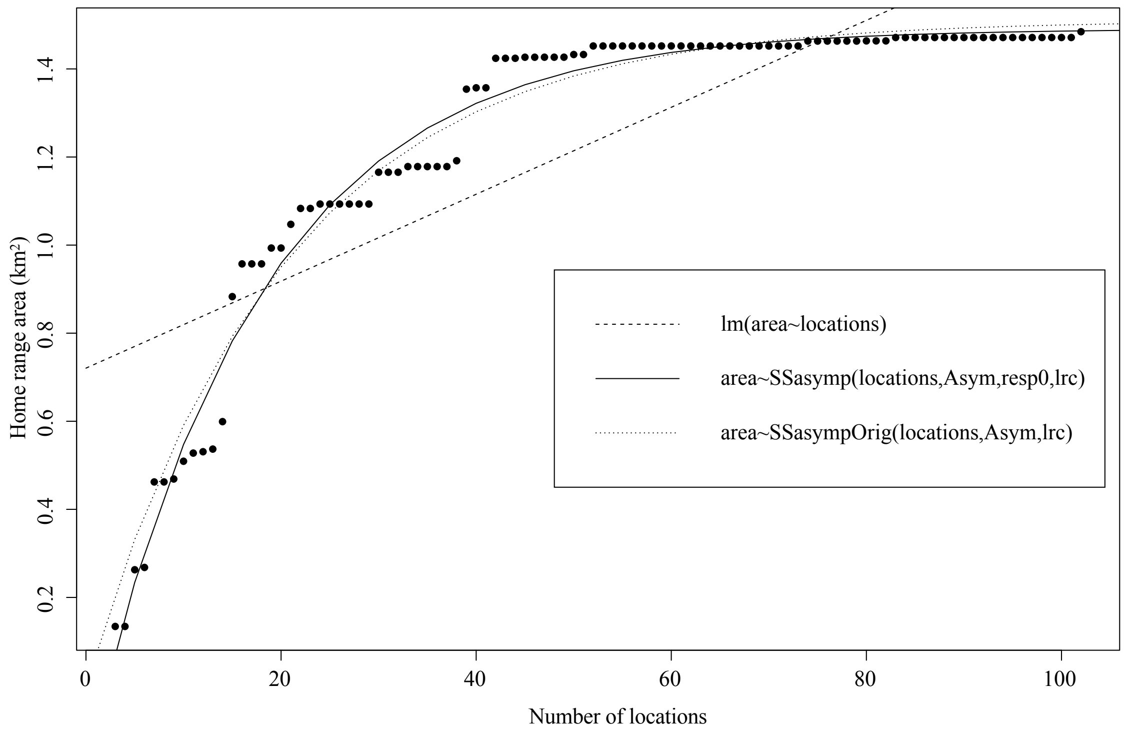


Figure 3.12 Performance of Incremental Area Analysis curves (solid black circles) generated for Group B wet season home range dataset against three regression models -caption as per Figure 3.10.

Logically, zero data points will support a home range estimate of zero, so the two-parameter exponential model (passing through the origin) was used to ascertain the sample size at which the Group B home ranges stabilised, despite the better statistical performance of the three-parameter model. The two-parameter model indicated that the yearly home range estimate stabilised after the inclusion of 110 locations (asymptote 'Asym'=1.50±0.010 and rate constant 'lrc'=-2.91±0.040, *n*=208; Figure 3.10), indicating the minimum sample required to accurately capture the group's yearly home range using the employed sampling protocol. The seasonal ranges, whether almost as large as the yearly home range, as for the wet season range, or slightly smaller, as for the dry season range, seemed to require slightly fewer locations to arrive at a robust estimate. The two-parameter model converged after the inclusion of 90 locations for the dry season (Asym=0.82±0.009 and lrc=-2.43±0.062, *n*=106; Figure 3.11) and 100 locations for the wet season (Asym=1.51±0.010 and lrc=-3.00±0.026, *n*=102; Figure 3.12). Together, the results of this analysis indicate that estimates derived for Group B from the yearly and seasonal datasets are likely to be valid and robust estimates for the home range requirements of this group.

Geographic concordance

Geographic concordance of the different estimates of Group B's home range was generally good, with all of the pair-wise estimate comparisons for the Group B yearly home range estimates exhibiting >50% spatial overlap, and almost half showing spatial concordance of 75%

or greater (Table 3.6). As expected, concordance was best between estimates that were variants of the same method, or those estimates generated by methods utilising similar computational approaches, with 78% overlap between the two KDE estimate variants, 95% between the two LoCoH variants, and >80% overlap between the MCP and LoCoH estimates (both variants). The concordance of estimates derived using vastly different statistical approaches was only slightly less however, with overlaps between the MCP and both KDE estimates and between the KDE h-LSCV and BBMM estimates all being ≥75%. This relatively modest difference in the geographic extent of these yearly Group B estimates is clear when the polygons of each estimate are considered (Figure 3.5).

The group's dry season estimates showed a similar pattern (Table 3.7, and see Figure 3.6). In fact, many estimates exhibited even greater spatial concordance, particularly those estimate-variant comparisons and the MCP-LoCoH comparisons already highlighted, which all showed ≥80% spatial concordance. Similarly, concordance between the BBMM estimate and each of the MCP and two KDE variants was generally better (≥77%), indicating the overall superior concordance of the dry season estimates. Spatial concordance of the wet season estimates was less impressive however, with almost half of the pair-wise estimate comparisons falling below 50% of spatial overlap and only the MCP and BBMM estimates showing >75% overlap (Table 3.8). This is apparent in the substantially different spatial extents of the different home range polygons (Figure 3.7), and explains the high variation observed in the size of the wet season home range estimates (Table 3.2).

Table 3.6 Geographic concordance between estimates of Group B yearly home range: percentage of overlap between estimate pairs (calculated against the larger of two estimates), with area of overlap in km^2 given in parenthesis. Poor spatial concordance (<50%) is indicated by *italicised* values, and good concordance (>75%) by **emboldened** values.

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

Table 3.7 Geographic concordance between estimates of Group B dry season home range: percentage of overlap between estimate pairs (calculated against the larger of two estimates), with area of overlap in km^2 given in parenthesis. Poor spatial concordance (<50%) is indicated by *italicised* values, and good concordance (>75%) by **emboldened** values.

Estimate	**MCP**	**KDE-LSCV**	**KDE-PLUGIN**	**k-LoCoH**	**a-LoCoH**
MCP	~	~	~	~	~
KDE-LSCV	64.5% (0.89)	~	~	~	~
KDE-PLUGIN	70.3% (0.80)	**83.2%** **(1.14)**	~	~	~
k-LoCoH	**85.6%** **(0.77)**	55.6% (0.76)	62.2% (0.71)	~	~
a-LoCoH	**80.6%** **(0.72)**	52.3% (0.72)	61.2% (0.70)	**90.2%** **(0.69)**	~
BBMM	**89.5%** **(0.80)**	**77.0%** **(1.06)**	**78.8%** **(0.94)**	56.2% (0.67)	52.4% (0.63)

Table 3.8 Geographic concordance between estimates of Group B wet season home range: percentage of overlap between estimate pairs (calculated against the larger of two estimates), with area of overlap in km^2 given in parenthesis. Poor spatial concordance (<50%) is indicated by *italicised* values, and good concordance (>75%) by **emboldened** values.

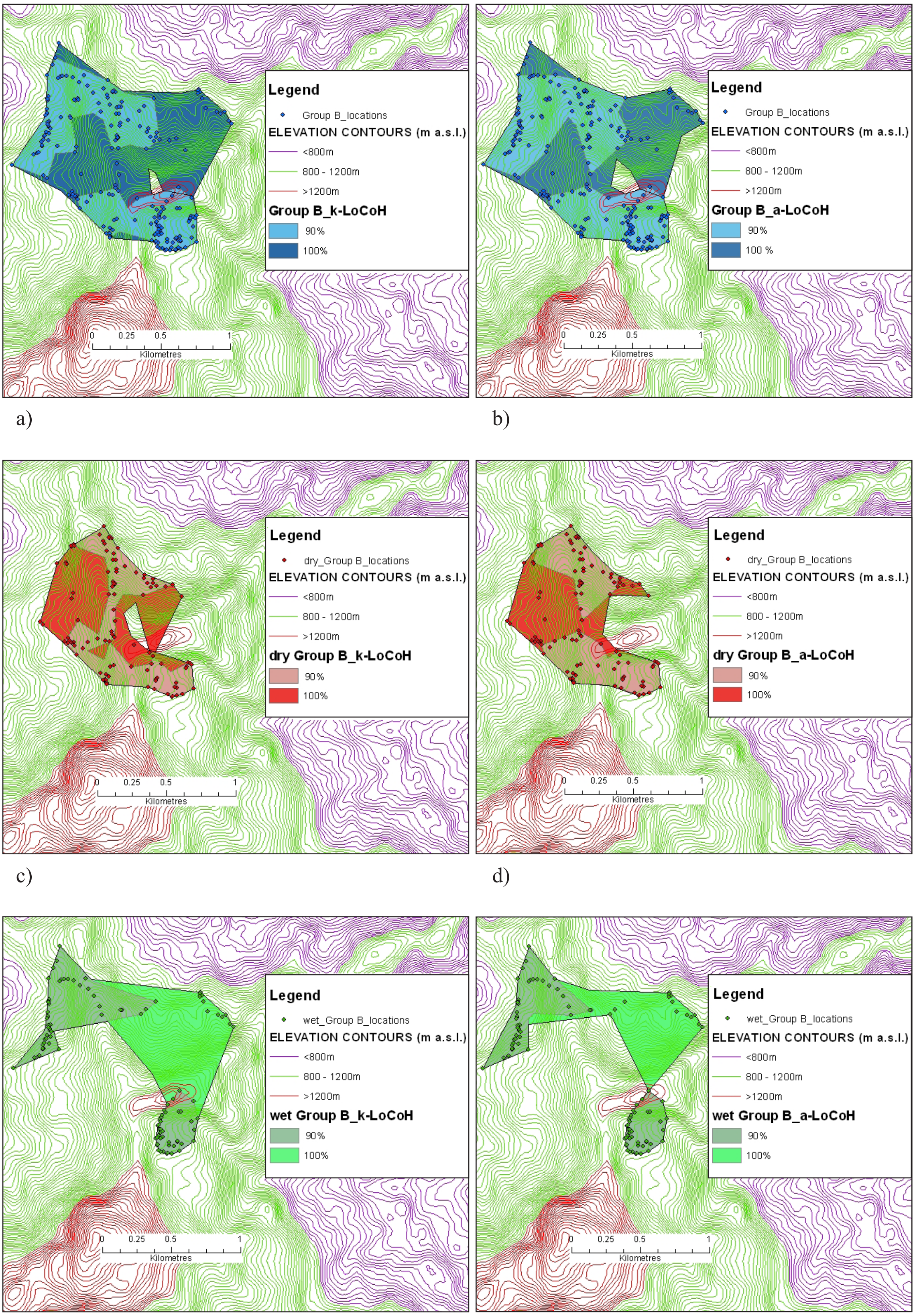
Estimate	**MCP**	**KDE-LSCV**	**KDE-PLUGIN**	**k-LoCoH**	**a-LoCoH**
MCP	~	~	~	~	~
KDE-LSCV	60.6% (1.38)	~	~	~	~
KDE-PLUGIN	55.9% (0.83)	52.4% (1.19)	~	~	~
k-LoCoH	56.9% (0.84)	*33.4%* *(0.76)*	*46.6%* *(0.55)*	~	~
a-LoCoH	*44.2%* *(0.66)*	*26.4%* *(0.60)*	*40.9%* *(0.49)*	74.9% (0.63)	~
BBMM	**78.4%** **(1.35)**	68.4% (1.55)	56.3% (0.30)	*47.8%* *(0.01)*	*37.1%* *(0.64)*

As expected, for Groups A and C the geographic concordance of the estimates was generally poor, with spatial overlap between estimates generally ≤50%. Only variants of the same estimation method showed substantial spatial overlap, e.g. approximately 62% (1.57 km^2) between the two KDE variants (h-LSCV and h-PLUGIN) for Group A, and around 92% (0.19 km^2) between the KDE variants, and 72% (0.06 km^2) between the two LoCoH variants (fixed, adaptive) for Group C (data not shown). This poor spatial concordance is again evident in the individual polygons (Figures 3.8, 3.9).

Performance of estimates against relevant landscape features

The k-LoCoH and a-LoCoH estimates of Group B yearly home range each produced polygons occurring entirely above 800 m a.s.l., with clear holes that corresponded approximately to areas of higher elevation (>1,200 m a.s.l.) in the landscape which the group is thought to not utilise (Figure 3.13 a) and b)). It is possible that the lack of exact concordance is a result of the imprecise nature of the method used to generate the elevation contours used for this assessment, which involved more than one step of interpolation, or due to assumptions made by the model about space between the collected locations in this area. The ability of the LoCoH estimation method to handle this interior 'hole' in the home ranges was better displayed by the seasonal home range polygons. The dry and wet season LoCoH polygons (both variants) each excluded the higher-elevation areas, and incorporated the reciprocal areas to east and west sides of the hole respectively (Figure 3.13 c)-f)). The a-LoCoH approach was slightly more successful in excluding the higher-elevation areas than the k-LoCoH polygons for both seasons. Again, these polygons also excluded lower elevations (<800m), and additionally provide a clear picture of the seasonal partitioning of the overall home range by the group.

Every other estimation method generally failed to exclude higher-elevation areas from either the yearly or seasonal estimates for Group B, instead assuming the gaps indicated by the LoCoH estimates were part of the group's home range (data not shown). This would account for the larger estimates reported by these estimates relative to the LoCoH home ranges (Figure 3.2). The poor performance of the BBMM model in particular is surprising, given that theoretically it should exclude areas that the group does not use by excluding areas not traversed directly (as indicated by the trajectory of collected locations). This may be a result of temporal breaks in the continuity of the collected ranging data, meaning the data comprised of several small sequential trajectories rather than a single continuous one, although as yet the robustness of this technique to such temporal inconsistencies is not well known. Regardless, if we regard the exclusion of areas of non-use as crucial to the reliability of the estimation of home range, then the LoCoH estimates can be regarded as the most reliable estimates of the Hainan gibbon's home range requirements.



a) b)

c) d)

e) f)

Figure 3.13 LoCoH estimates of Group B year (a, b); dry (c, d); and wet season (e, f) home range produced by k-LoCoH (a, c, e) and a-LoCoH (b, d, f) estimation viewed against elevation contours extracted from the DEM (10m intervals). Gaps in the LoCoH polygon coincide (approximately) with elevations of >1,200 metres above sea level (m a.s.l.), as indicated by red contour lines. Green contour lines correspond to elevations 800-1,200 m a.s.l., and purple contour lines to elevations <800 m a.s.l.

Discussion

Hainan gibbon home range requirements

The rigorous spatial analyses employed here indicate a yearly home range of 1-2 km^2 for a Hainan gibbon social group, with 1.49 km^2 representing the figure closest to the median of all estimates derived. This study therefore revealed the home range requirements of the species to be much smaller than the c.10 km^2 estimates previously reported and held to account for the species' limited population growth (Zhou et al. 2008a, Zhou et al. 2008b, Li et al. 2010). My findings, which are the most robust estimates of Hainan gibbon spatial requirements reported to date, indicate that the previous large figures have substantially overestimated the species' home range and, given the paucity of information regarding data collection and estimation techniques, those figures are unreliable. In contrast, using a number of analytical approaches I was able to determine that the ranging data collected for Group B are representative, and the estimates derived from these data are valid and reliable. These methodologically transparent estimates therefore constitute a robust representation of the species' home range.

The revised home range estimates produced in this study are not only more robust, they are also more consistent with estimates reported for other closely related crested gibbon species. The Cao Vit gibbon has a reported mean home range of 1.3 km^2 (Fan et al. 2010, Fei et al. 2012), and the home range of the *N. concolor* population in the Wuliang Mountains of central Yunnan, China, is estimated at 1.51 km^2 (Fan and Jiang 2008a). For the latter population, if gaps within the home range boundary constituting areas where gibbons were not observed are excluded, then the estimate is closer to 1.30 km^2. This aligns very closely with the LoCoH estimates derived for Group B's yearly home range (k-LoCoH: 1.34 km^2; a-LoCoH: 1.28 km^2), which were demonstrated to successfully exclude internal high-elevation areas within the group's home range that the gibbons are less likely to utilise. These specific comparisons are particularly pertinent, given the phylogenetic proximity and ecological similarity of both of these species to the Hainan gibbon. The populations from which these reported estimates are derived occur at similar latitudes, occupy similar seasonal high-altitude forests, and are subject to the same pressures of small population size, limited available habitat and reduced habitat quality (Jiang et al. 2006, Fan and Jiang 2008a, Mootnick et al. 2012, Fan et al. 2013b), and both species are also listed as Critically Endangered (IUCN 2013). Other *Nomascus* species, which are less vulnerable to these pressures, appear to have home ranges that are similar to non-crested gibbons (average home range: 0.35 km^2, after Chivers et al. 2013); e.g. *N. siki* (0.38 km^2, Rowe and Myers 2011), *N. leucogenys* (0.40 km^2; Julia Ruppell pers. comm., April 2013), *N. gabriellae* (0.60 km^2; Marina Kenyon pers. comm., April 2013). Whether the larger home ranges of the Critically Endangered *Nomascus* gibbons represent a response to their ecological situation, or an intrinsic trait shown by these representatives of the genus, remains to be seen.

Overall, however, I found no evidence that the Hainan gibbon exhibits exceptional ranging behaviour or has an extreme home range when considered in the context of other, closely related crested gibbons in similar environmental conditions.

Seasonality and group overlap

Group B was found to use around 0.71 km^2 or approximately 50% of their yearly home range in both seasons, and there was evidence that the group not only utilises different parts of the landscape in the wet and dry seasons, but also that the overall extent of the wet season home range may be slightly larger than in the dry season. Seasonal differences in range extent could reflect seasonal differences in food availability. Raemaekers (1980) demonstrated that white-handed gibbons (*Hylobates lar*) adopt a 'loss-cutting' policy when food abundance is low, reducing their range use compared to when food is plentiful. It is not clear exactly how the availability of food within BNNR varies with season, but it has been reported that February-April is the most food-poor (and species-limited) time of year for the gibbons (Chan et al. 2005), which corresponds to the end of the dry season as sampled in this study. Most importantly, as the estimates reveal different areas are utilised in different seasons, it is clear that a year-long home range is most appropriate for accurately describing the species' spatial requirements when considering potential management actions.

Insights into tolerated group home range overlap were limited by the relative uncertainty of the other group home range estimates. Overlap between groups A and B was seemingly small, corresponding to between 6-17%. This does not, however, differ greatly to the amount of overlap between neighbouring Cao Vit gibbon groups, where mean home range overlap is 16.8% (range: 12-22%; Fei et al. 2012), or non-crested gibbon groups; *Hylobates moloch*: 12% (Kappeler 1984) and *H. albibarbis*: 15-25% (Cheyne et al. 2008), although *H. lar* groups tolerate closer to 30% overlap (Reichard and Sommer 1997, Bartlett 1999). Despite the reduced reliability of the Group A home range estimate, it appears that group range overlap in Hainan gibbons is therefore closely comparable with estimates for other gibbons.

Drivers of ranging patterns

Ranging of Hainan gibbon groups is likely to relate to a number of underlying landscape features, including physical attributes such as food tree distribution, elevation and rivers, as well as anthropogenic modification and disturbance of the landscape (e.g. roads, power lines, agricultural incursion). The LoCoH estimates, which were able to exclude higher elevations from the Group B home ranges and indicated only areas above 800 m a.s.l. were utilised, support the reported preference for forest between elevations of 800-1,200 m a.s.l. (Liu and Tan

1990). This provides some evidence for elevation being a potential driver of gibbon home ranges. The ranges reported by the other estimates predominantly included the higher elevation areas within the group's range. However, this is more likely to reflect the inability of these models to accommodate such features (Getz and Wilmers 2004) than the absence of such habitat preference. Unfortunately, beyond this simple assessment, it was not possible to obtain sufficiently high-resolution data on other landscape features to assess the specific effects such factors may have upon the species' space use. Habitat assessment data reportedly exist for BNNR (Bosco Chan pers. comm., September 2013), but it was not possible to access these data during this study due to political and cultural constraints. A crucial next step therefore is to relate observed gibbon ranging patterns to underlying habitat features to identify the primary environmental drivers of Hainan gibbon ranging. This analysis will permit a more informed assessment of the forest management required within BNNR to enhance the landscape to support gibbons. Understanding the predictors of ranging will also be vital to assess potential habitat suitability outside the reserve when considering more intensive population management actions (e.g. translocation).

Limitations and reliability of home range estimates

It is apparent from my investigation that sample size, sampling duration, and estimation technique will all alter our estimate of home range. The influence of reduced sample size was clear for the home range estimates derived for the two unhabituated social groups (Groups A and C), which were based upon very modest datasets and as a result showed marked variation with estimation approach and poor geographic concordance of the resultant ranges. Based upon the IAA, it is likely that the datasets collected for these shy and evasive groups were not representative, which is not surprising given the sample sizes compared to the minimum samples required to detect Group B's yearly and seasonal home ranges revealed by the same analysis.

Together, the analyses indicate that only the Group B estimates are reliable. The estimates of this group's ranges also varied depending on the method used. This variation between estimate forms was expected, as the four different estimation approaches employ distinct mathematical approaches to predict home range size, based upon different theoretical and biological assumptions. This manifests predominantly in the decisions made by each model about the use of space between and around collected locations and whether these areas are ultimately included in the home range or not, which is acutely apparent for areas of high elevation. Estimate variation did however decrease with increasing sample size, from 71.1% difference between the smallest and largest estimates for the wet season home range (where n=102), to 46.7% for the dry season (where n=106), and only 33% for the overall (yearly) Group B estimate (n=208).

The yearly dataset also showed the greatest spatial concordance, indicating that as more locations are included, the different approaches will converge upon the extent and geographic location of home range. The influence of sample size upon estimate magnitude is well documented (Boyle et al. 2009, Lichti and Swihart 2011), as is the effect of estimation technique (Harris et al. 1990, Grueter et al. 2009b), indicating that a home range estimate is explicit to what we define it as, and it is therefore vital to report methods in full when reporting home range.

The seasonal differences detected in the size and geographic location in Group B's home range extent also indicate that specifying the temporal scale of data collection is crucial when reporting a home range estimate. The consequence of sampling duration on home range estimation remains largely unexplored in the literature compared to the effects of sampling intensity (frequency of location collection) and sample size (but see Girard et al. 2002, Moland et al. 2011). I have been explicit about the sampling protocol and effort (duration and observation success rate) that produced the final locational datasets for home range estimation. Past studies describing the Hainan gibbon's ranging requirements have generally failed to report one (or all) of these parameters, and often crucially the home range analysis method employed when estimating home range. For example, Liu and Tan (1990) reported an observation frequency of 10 days per month during their year-long study but did not detail the frequency of location collection, observation success rate or overall sample size of the dataset upon which they based their estimate of 2-5 km^2, nor the computational approach adopted. It is likely that the largest reported estimates, 5.48-9.87 km^2 (Fellowes et al. 2008, Zhou et al. 2008a) represent a conflation of home range size and probable home range shift over time. These estimates are reportedly based upon daily tracking of groups over an observation period of 2002-2006, constituting 220 days of observations (Zhou et al. 2008a), but the frequency (and duration) of location collection and the statistical approach used to derive the estimates are again not made explicit. If the reported estimates are based on location data collected over this entire, extended period, then these estimates may have captured changes in space use patterns that are likely to have occurred between years, leading to large overall estimates of home range and an overestimate of the species' spatial requirements relative to other gibbons. My estimates, based upon data collected over a total of 93 days spread over approximately 12 months, are directly comparable to those derived for the Wuliang Mountain *N. concolor* population, which were based upon a total of 125 days of data collection over 14 months (Fan and Jiang 2008a), and for *N. nasutus*, derived from just over one year's data (September 2008-December 2009) (Fan et al. 2010). Controlling for sampling duration thus revealed that the Hainan gibbon does not have extraordinary spatial requirements compared to closely related species in similar ecological contexts.

Management implications: Home range as a potential constraint to population growth

The more modest home range requirements revealed in this study have important implications for the conservation management of the Hainan gibbon. As an area of suitable gibbon habitat will usually be saturated with social groups in a tight mosaic of closely interlocking home ranges (Reichard and Sommer 1997), home range, in combination with the amount of overlap tolerated, is crucial to understanding the capacity of the habitat to support multiple social groups. If we consider the previous 9.9 km^2 estimate of home range (Zhou et al. 2008a, Zhou et al. 2008b, Li et al. 2010), then (allowing for 17% overlap between groups) the c. 15 km^2 of available habitat will only support a total of 1.8 groups and 11.6 gibbons (assuming an average group size of 6.33; pers. obs., August 2011; BNNR Management Office pers. comm., March 2014). This would suggest that the habitat is now at saturation. However, this is unlikely to be the case in reality, given that the population reportedly reached 24 individuals in 2009 (Li et al. 2010) and has remained close to this for the last four years (BNNR Management Office, pers. comm., March 2014). Adopting an exclusive group home range of 1.25 km^2 (1.5 km^2 excluding 17% overlap), the same area could support around 76 gibbons in 12 groups. This is not presently the case, but this estimation is important, as it suggests that home range and the amount of available habitat *per se* may be playing less of a role than previously argued in constraining population growth, and the recent lack of population increase may be due to other factors (e.g. genetic relatedness, lack of available mates). This is not to suggest that other habitat features (level of disturbance, condition) may not be impacting the population, or that enhancing and increasing the available habitat is not a conservation priority. Preventing further degradation of the remaining habitat within BNNR is crucial to the survival of both the Hainan gibbon and a suite of other endemic species that occur within the reserve, and if the population is to thrive, not just survive, a substantial increase in habitat is required. However, taking into account this new sound and systematic evidence about the species' home range, and clarification of its potential influence on gibbon population dynamics, it seems that attention should now be directed to elucidating the role of other possible constraining factors that may be of prime importance in constraining population growth in the species.

Chapter 4. Present and past genetic status of the Hainan gibbon: identifying effects and consequences of sustained reduction in population size

Introduction

Following a precipitous decline from an estimated 2,000 individuals in the 1950s (Liu et al. 1984), to a reported low of only 10 individuals by the early 1990s (Zhang 1992), the Hainan gibbon has persisted for over 30 years at an exceptionally low population size, with population estimates since the 1980s fluctuating between around 10 and 25 individuals. The current population consists of an estimated 25 individuals in three social groups: Group A (c. eleven individuals); Group B (seven individuals); and Group C (three individuals); together with a low, unknown number of solitary individuals (pers. obs., August 2011; BNNR Management Office pers. comm., March 2014). When a population experiences such marked decline in population size (population bottleneck), it is also likely to experience a concomitant loss in genetic diversity (genetic bottleneck). Small populations are more vulnerable to loss of genetic diversity as a result of factors that have only a minimal impact in large populations, but the effects of which become substantial in small populations; namely chance loss of alleles, or ‘genetic drift’, leading to loss or fixation of alleles (Frankham et al. 2009). This is of particular concern for deleterious alleles, which generally exist in small frequencies in large populations as they are selected against, but can become more influential in small populations as the effects of selection are reduced or even eliminated, and stochasticity dominates evolution (Frankham et al. 2009). In addition, although individuals in a small population may still mate randomly, there is an increased probability of mating between related individuals, as the pool of available mates is smaller, resulting in accelerated inbreeding in small populations and a further decline in genetic variation.

Many threatened species have experienced bottlenecks and exhibit reduced genetic diversity as a result. The Mauritius kestrel (*Falco punctatus*) suffered a population bottleneck of a single pair in 1974, and while it has recovered in terms of population size (400-500 individuals by 1997), it still shows a reduced level of genetic diversity compared to other populations of non-endangered kestrel species (Groombridge et al. 2000). Similarly, the European bison (*Bison bonasus*) was hunted to extinction in the wild by 1925 and the current wild population of re-introduced individuals, which were captive-bred from a limited zoo population, exhibits extremely low genetic variation (on average 2.3 alleles/locus) (Luenser et al. 2005). This is lower still than the diversity of its sister species, the American bison (*Bison bison*), which also shows reduced allelic variation (on average 5-16 alleles/locus) as a result of a bottleneck of around 300 individuals in the late 1800s (Schnabel et al. 2000).

Reduced genetic diversity can have direct implications for the long-term survival of a diminished population, and in the case of the Hainan gibbon, where only one population persists, the species. A decline in genetic variation can result in reduced ability to withstand sudden changes in the environment, compromised resistance to disease, and reduced survival and reproductive fitness of offspring ('inbreeding depression') (Soulé et al. 1986, Soulé 1987). For example, the Tasmanian devil (*Sarcophilus harrisii*) has suffered repeated population bottlenecks, including one in the early 1800s due to extensive hunting, and despite recovering to tens of thousands of individuals by the 1990s, the species is currently threatened with extinction due to poor resistance to the newly emerged Devil Facial Tumour Disease (DEH 2006). The present devil population exhibits greatly reduced variation in the major histocompatibility complex (MHC) gene, meaning that devil cells do not recognise foreign tissues and do not mount an immune response when compromised by tumour cells, which has led to a rapid and widespread decline of the species (Siddle et al. 2007). Genetic factors can therefore clearly increase a population's vulnerability, and the genetic state (or 'health') of a species must be understood before appropriate management actions can be identified and implemented.

Despite the Hainan gibbon's Critically Endangered status, past genetic research for the species has predominately consisted of its inclusion in analyses investigating the phylogeny of the Hylobatidae (Su et al. 1995, Zhang 1995, Thinh et al. 2010a, c). Several authors have alluded to the genetic consequences of small population size when discussing the situation of the Hainan gibbon, and have indeed argued that the surviving population is likely to be suffering from genetic constraints (Liu et al. 1989, Fellowes et al. 2008). Reports of nine of 12 offspring born between 1982-1989 being male have led to concerns that the population is exhibiting an imbalanced sex ratio (Liu et al. 1989), which is thought to be limiting mate availability, and consequently social group formation and population growth (Chan et al. 2005, Li et al. 2010). Crucially, the species exhibits no obvious sexual dimorphism prior to reproductive maturity (at c. 6-7 years), making it impossible to accurately sex immature individuals through visual observation, which casts doubt on past reports of offspring sex. Assumptions have also been made about incest and inbreeding within the population constraining population growth, with concern that most surviving individuals are very closely related (Liu et al. 1989, Zhou and Zhang 2003, Fellowes et al. 2008). However, to date, there has only been one attempt to investigate the genetic status of the species, through an assessment of diversity in the mitochondrial DNA (mtDNA) control region (Li et al. 2010). Unfortunately, there are number of methodological issues associated with this work that minimise its utility in understanding the species' current genetic health. These include sampling limitations (n=6 individuals) which restrict representativeness, possible sequencing errors indicated by detection of four haplotypes in one social group, and failure to contextualise the results in terms of other gibbon species' genetic diversity or, more pertinently, past levels of diversity of the Hainan gibbon. Furthermore, the study provided no insights into fundamental demographic parameters of the current population, such as relatedness of individuals, level of inbreeding, and offspring sex ratio. As such, these factors, which are crucial to understanding the population's viability, remain unknown.

A paucity of information regarding the genetic health of the remaining Hainan gibbon population is precluding an accurate appreciation of the role this factor may be playing in constraining population recovery. A comprehensive and careful assessment of the species' current genetic diversity within the context of its past genetic diversity is vital to inform conservation planning for the species. This study therefore aimed to quantify the genetic diversity of the current population and assess any decline in diversity that may have occurred as a result of the observed historical reduction in population size. To do so, I determined the present and past genetic diversity of the species and any genetic differentiation between these temporal 'populations', evaluated the genetic evidence for inbreeding and past genetic bottleneck, and estimated the effective population size of the current population in comparison to that of the historical. Empirical data on population parameters which have genetic and demographic consequences are also required if the current status of the species is to be accurately appreciated. Therefore, I also assessed key characteristics of the current population, including the degree of relatedness and sex ratio of the population (and offspring only). This thorough assessment therefore improves our understanding of the possible influence the species' current genetic condition may have on its long-term viability.

Methods

Data collection

Sample collection

Faecal samples were collected opportunistically from the current population during tracking of social groups within BNNR in 2010-2011 for ranging data collection (see Chapter 3). Samples were collected immediately following observed defecation events. All individuals of habituated Group B (seven, as at September 2011, hereafter 'B1'-'B7') were sampled, several more than once while, due to limited contact time, only single samples were collected from one individual from each of the two unhabituated groups (hereafter 'A' and 'C'), representing a sampling rate of 36% (nine of the estimated 25 individuals in the population). Faecal samples were preserved by adding silica gel beads (drying-agent) to approximately 2-5 g of scat in a 15 ml plastic tube (as per Wasser et al. 1997, Goossens et al. 2003, Chambers et al. 2004). Beads were regularly replaced upon saturation until samples were completely desiccated. Where available, additional sample material was kept in a replicate silica-dried sample, and any remaining material was preserved in 70% ethanol. Samples were stored in cool dark conditions in the field and at 4 °C in the laboratory until DNA extraction.

To assess the historical genetic diversity of the species, small samples (c. 5 mm x 2 mm) of skin, muscle or bone tissue were collected from a total of 12 Hainan gibbon specimens available in museum collections (Table 4.1). The samples obtained represent all but one of the confirmed *hainanus* specimens known at the time of this study (it was not possible to destructively sample the holotype). The sampled specimens were accessioned between 1899 and 1980, thus the historical sample set spans a period of 81 years. Samples were stored in paper envelopes until extraction. While every precaution was taken to prevent human contamination during sampling, to monitor any possible contamination, hair samples (c. 10 freshly-plucked hairs) were also collected from all field sample collectors. These samples also acted as positive controls during DNA amplification. Blood samples from modern captive specimens of two species of gibbon, *Hylobates lar* and *Nomascus concolor* (source: Zoological Society London Blood and Tissue Bank), were used as positive controls.

DNA extraction

Genomic DNA was extracted from faecal samples using the QIAamp DNA Stool kit (QIAGEN), with minor protocol modifications to enhance removal of impurities/inhibitors and increase DNA yield (overnight lysis soak, extended exposure to InhibitEX reagent, prolonged final buffer incubation). A final elution volume of 120 µl was used to improve DNA concentration. For individuals where >1 sample was collected, multiple samples were extracted. As DNA is not spread uniformly through faecal samples (Goossens et al. 2003), where sample volume permitted, multiple independent extractions were taken to maximise probability of obtaining DNA. DNA was extracted from historical skin/muscle samples using the QIAamp DNA Micro kit (QIAGEN), and from bone samples using the QIAquick PCR Purification kit (QIAGEN). A final elution volume of 100 µl and post-elution addition of 5 µl of 1% TWEEN (Sigma-Aldrich) were employed to increase DNA concentration. DNA was extracted from control gibbon blood and human hair samples using the DNeasy Blood & Tissue Kit (QIAGEN). Rigorous standard procedures were employed to minimise likelihood of contamination, including: stringent cleaning of all surfaces and equipment (with 40% bleach and/or exposure to ultraviolet radiation); extraction of samples for different individuals on separate occasions; and extraction of modern, historical and control samples in physically separate laboratory areas in specialised facilities at Yunnan University, Kunming, China, the Institute of Zoology (Zoological Society of London), and Royal Holloway University of London.

Table 4.1 Existing museum specimens of *Nomascus hainanus* sampled for assessment of the historical genetic state of the species, with details of samples collected.

Year	**Museum/Collection**	**Specimen accession number**	**Species (as listed in museum catalogue)**	**Locality information**	**Specimen type**	**Sample type**
1899	National Museum of Ireland, Dublin	NMINH:1899.51.1	*Hylobates hainanus*	China	skin (mounted specimen) and skull	skin tissue and bone fragments
1891	Natural History Museum, London	ZD.1891.12.10.1	*Hylobates concolor hainanus*	Hainan [19°00' N, 109°30' E]	skin (mounted specimen) ***Holotype***	***SAMPLE NOT PERMITTED***
1893	Natural History Museum, London	ZD.1893.9.12.1	*Hylobates concolor hainanus*	Hainan [19°00' N, 109°30' E]	skin and skull (and skeleton)	skin tissue
1907	Natural History Museum, London	ZD.1907.12.1.1	*Hylobates concolor hainanus*	Hainan [19°00' N, 109°30' E]	skin	skin tissue
1911	Natural History Museum, London	ZD.1911.2.24.4	*Hylobates concolor hainanus*	Hainan [19°00' N, 109°30' E]	skin and skull	skin tissue
1909	Museum für Naturkunde, Berlin	Inv. No. 84622	*Nomascus concolor hainanus*	Hainan	skin and skull	skin tissue
1909	Museum für Naturkunde, Berlin	Inv. No. 85357	*Nomascus concolor hainanus*	Hainan ("Hoi Chow")	skin	skin tissue
1962	South China Institute of Endangered Animals, Guangzhou	0088	*Hylobates concolor hainanus*	Jianfengling, Hainan	skin and skull	hairs with residual skin tissue
1964	South China Institute of Endangered Animals, Guangzhou	0502	*Hylobates concolor hainanus*	Bawangling, Hainan	skin (mounted specimen) and skull	dried muscle tissue and bone fragments
1964	South China Institute of Endangered Animals, Guangzhou	0503	*Hylobates concolor hainanus*	Bawangling, Hainan	skin and skull	skin tissue and bone fragments
c. 1960s	South China Institute of Endangered Animals, Guangzhou	uncatalogued	unlabelled (reportedly *N. hainanus*)	unknown (uncatalogued), likely Bawangling	post-cranial bones	dried muscle tissue
1980	Haikou University/BNNR Management Office, Hainan	671	*Nomascus hainanus*	Bawangling, Hainan	skin (with skeleton)	skin tissue and bone fragments
1980	Haikou University/BNNR Management Office, Hainan	672	*Nomascus hainanus*	Bawangling, Hainan	skin (with skeleton)	skin tissue and bone fragments

Microsatellite primer screening

Microsatellite loci are short, tandem nucleotide sequences of 2-6 base pairs (bp) repeated up to 100 times in eukaryote genomes (Tautz 1993). The high degree of polymorphism and high mutation rate of microsatellites make them widely-used markers for investigating genetic diversity, population structure, relatedness etc. in conservation genetics studies (Wayne and Morin 2004). As faecal and historical museum samples often yield highly-fragmented (short bp fragments) and low concentration DNA extractions, microsatellites were particularly practical. No gibbon-specific microsatellite primers currently exist, therefore I adopted a cross-species amplification approach (Goossens et al. 2000b, Vigilant and Bradley 2004, Goossens et al. 2005), amplifying gibbon DNA using human-derived microsatellite primers. It was necessary to screen a selection of available human microsatellite primers to obtain a sufficient set of successfully-amplified, polymorphic loci for calculation of relevant population genetics measures.

Thirty human microsatellite loci (Table 4.2) that had previously been tested for *Hylobates lar* and *Hylobates muelleri* (Watanabe et al. 1997, Crouau-Roy 1999, Clisson et al. 2000, Oka and Takenaka 2001, Chambers et al. 2004, Roeder et al. 2009), which were smaller than 250 bp, were screened. This size threshold was adopted as loci larger than this have been shown to be problematic when amplifying DNA sourced from non-invasive samples, including from apes (Goossens et al. 2000b). Loci previously found to be monomorphic or to not amplify in these two other gibbon species were not excluded, as successful cross-amplification of a given locus appears to be species-specific (Table 4.2). DNA extractions from three individuals in the current population (constituting the greatest extraction volumes and corresponding to 33% of the sampled population) and the two control gibbon species samples were used to test loci.

DNA samples were amplified using loci primer pairs via polymerase chain reaction (PCR) amplification in a reaction volume of c.7 µl containing 2 µl (≤50 ng, exact amount variable) of template (extracted) DNA, 0.5 µl (0.3 µ*M*) of primer, 0.02 µl bovine serum albumin (New England Biolabs), and 3.5 µl of Multiplex PCR Mix (QIAGEN, final concentration of 3 m*M* $MgCl_2$). Primers were screened individually ('singleplexed'), without fluorescent labelling. The thermal profile for all PCR reactions consisted of: initial denaturation at 95° C for 15 minutes; 30-35 cycles of denaturation at 94° C for 30 seconds; annealing at the relevant annealing temperature for 90 seconds (see Table 4.2 for locus-specific temperatures); extension at 72 °C for 60 seconds; followed by a final extension at 72 °C for 30 minutes. Products were visualised using the Qiaxcel DNA Screening Kit (QIAGEN) which does not require primers to be fluorescently labelled.

Table 4.2 Details of human microsatellite loci screened. 'Method' refers to whether loci were tested only at screening phase (Qiaxcel) or fully genotyped (Sequenced). Where 'no amplification' is reported, the locus failed to produce products for all *N. hainanus* samples (although it may have amplified for control gibbon species). PCR annealing temperatures reported for failed loci represent the lowest temperatures tested.

Locus	Repeat motif	Method	Annealing Temp. (°C)	No. PCR cycles	Result	Used in analysis	Previous use for gibbons	Gibbon species	Sample type	Approximate product size (bp)
D1S207	Di	Qiaxcel	50;48	15;20	*no amplification*	no	Clisson et al. (2000)	*Hylobates lar*	blood	128
D1S548	Tetra	Qiaxcel, Sequenced	53	35	**polymorphic**	yes	Chambers et al. (2004)	*Hylobates lar*	faecal	160-188
D1S550	Tetra	Qiaxcel, Sequenced	50	35	monomorphic	no	Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
D2S1329	Tetra	Qiaxcel, Sequenced	50	35	monomorphic	no	Chambers et al. (2004)	*Hylobates lar*	faecal	188-216
D2S1777	Tetra	Qiaxcel, Sequenced	46	35	*poor amplification*	no	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	190-230
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D2S367	Di	Qiaxcel, Sequenced	54	30	**polymorphic**	yes	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	102-170
							Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
D5S1457	Tetra	Qiaxcel, Sequenced	54	30	**polymorphic**	yes	Chambers et al. (2004)	*Hylobates lar*	faecal	130-154
D5S1470	Tetra	Qiaxcel, Sequenced	50	35	**polymorphic**	yes	Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
D5S807	Tetra	Qiaxcel, Sequenced	54	30	monomorphic	no	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	142-190
							Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
D6S265	Di	Qiaxcel, Sequenced	56;54	15;20	**polymorphic**	yes	Clisson et al. (2000)	*Hylobates lar*	blood	156
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D6S2972/ MOG-CA	Di	Qiaxcel	50;48	15;20	*no amplification*	no	Clisson et al. (2000)	*Hylobates lar*	blood	136
D7S503	Di	Qiaxcel	50;48	15;20	*no amplification*	no	Clisson et al. (2000)	*Hylobates lar*	blood	130
D7S817	Tetra	Qiaxcel, Sequenced	56;54	15;20	**polymorphic**	yes	Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
D8S1106	Tetra	Qiaxcel, Sequenced	46	35	*poor amplification*	no	Chambers et al. (2004)	*Hylobates lar*	faecal	no amplification
D9S302	Tetra	Qiaxcel, Sequenced	56;54	15;20	**polymorphic**	yes	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	180-230
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic

D10S1432	Tetra	Qiaxcel, Sequenced	46	35	*poor amplification*	no	Chambers et al. (2004)	*Hylobates lar*	faecal	152-198
D11S1984	Tetra	Qiaxcel, Sequenced	54	35	monomorphic	no	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	150-220
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D13S321	Tetra	Qiaxcel	*50*	35	*no amplification*	no	Chambers et al. (2004)	*Hylobates lar*	faecal	215-251
D14S255	Di	Qiaxcel, Sequenced	56;54	15;20	*poor amplification*	no	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	172-190
D14S306	Tetra	Qiaxcel, Sequenced	56;54	15;20	monomorphic	no	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	142-172
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D16S2624	Tetra	Qiaxcel, Sequenced	56;54	15;20	monomorphic	no	Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D17S804	Di	Qiaxcel, Sequenced	54	35	**polymorphic**	yes	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	130-150
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
D20S206	Tetra	Qiaxcel, Sequenced	53	35	**polymorphic**	yes	Oka & Takenaka (2001)	*Hylobates muelleri*	hair or faeces	100-120
							Chambers et al. (2004)	*Hylobates lar*	faecal	159-175
DQcar	Di	Qiaxcel, Sequenced	53	35	**polymorphic**	yes	Clisson et al. (2000)	*Hylobates lar*	blood	108-117
							Roeder et al. (2009)	*Hylobates lar*	muscle or hair	107-117
							Crouau-Roy (1999)	*Hylobates lar*	*not reported*	107-117
							Chambers et al. (2004)	*Hylobates lar*	faecal	monomorphic
DXS571	Di	Qiaxcel, Sequenced	56;54	15;20	monomorphic	no	Roeder et al. (2009)	*Hylobates lar*	muscle or hair	131-135
DXS8043	Di	Qiaxcel, Sequenced	56;54	15;20	**polymorphic**	yes	Roeder et al. (2009)	*Hylobates lar*	muscle or hair	173-175
DXYS156	Penta	Qiaxcel, Sequenced	58	30	**polymorphic**	yes	Roeder et al. (2009)	*Hylobates lar*	muscle or hair	116-126
HPRT1	Tetra	Qiaxcel, Sequenced	56;54	15;20	**polymorphic**	yes	Roeder et al. (2009)	*Hylobates lar*	muscle or hair	144-156
							Watanabe et al. (1997)	*Hylobates lar*	blood	sizes not reported
TNFa/b	Di	Qiaxcel	*50*	35	*no amplification*	no	Clisson et al. (2000)	*Hylobates lar*	blood	211
							Chambers et al. (2004)	*Hylobates lar*	faecal	poor amplification
vWF	Tetra	Qiaxcel	48	35	*no amplification*	no	Chambers et al. (2004)	*Hylobates lar*	faecal	no amplification

DNA amplification and genotyping

Twenty four microsatellite loci produced detectable PCR products for the Hainan gibbon DNA samples (Table 4.2) and were therefore used for formal genotyping. DNA samples were amplified using fluorescently labelled forward sequences for each primer pair over 30-35 cycles of PCR amplification, with PCR reagents and reaction concentrations as per the singleplexes. The 24 loci were divided into eight 'multiplex' mixes, each containing three loci, based upon the fluorescent dye, apparent product size (bp), and required annealing temperature of each locus. Some additional optimisation of annealing temperatures and mixes was necessary during replicate PCRs. PCR amplification products were visualised on an ABI PRISM 3130xl Genetic Analyser (Applied Biosystems) automatic sequencer together with GeneScan 500 LIZ Size Standard (Applied Biosystems). Alleles were scored using GeneMapper V.4.1 (Applied Biosystems) against the internal size standard to derive individual genotypes at each locus.

Genotypes were scored using a strict set of *a priori* rules following Taberlet et al. (1996) and Goossens et al. (2000a), whereby: a) alleles were only scored as true alleles if observed at least twice; b) both alleles of purported heterozygotes were genotyped at least twice before accepted as true heterozygotes; and c) purported homozygotes were genotyped five times before accepted as true homozygotes. Consensus genotypes for each individual were derived using multi-tube, multi-sample approach (Taberlet et al. 1996, Goossens et al. 2000a), with a minimum of five independent PCR replicates genotyped for each extraction to minimise genotyping problems associated with low-quality template DNA (e.g. false alleles, allelic dropout) (Taberlet et al. 1999). For modern population samples, I genotyped a minimum of three extractions per sample and two samples per individual, except for individual B6 and those individuals from Group A and Group C. Only single samples were obtained for these individuals, limiting genotyping replicates to multiple extractions. For historical samples, limited sample material prevented multiple extractions, therefore restricting replication to multiple PCR reactions only.

To ensure allele sizes were standardised between samples/replicates, current and historical sample PCRs were prepared in physically-isolated areas to prevent cross-contamination but amplified simultaneously (in the same PCR machine), and reference samples (a well-performing extraction from one modern sample) were included in every PCR. Positive (human and gibbon) and negative controls from every stage (extraction blanks, PCR blanks, sequencing blanks) were also included during genotyping to monitor potential contamination and PCR failure. Human and gibbon control alleles were generally observed to be different sizes to Hainan gibbon alleles, making it possible to immediately discount any positive control products. Thus it is unlikely any genotypes scored for Hainan gibbon samples correspond to erroneous human/non-target gibbon alleles. Modern sample genotypes were also verified by checking for consistent allele-sharing between individuals in the current population for which parentage was known.

Loci monomorphic for the Hainan gibbon, and those that failed to amplify despite extensive replication, were discounted from the dataset, resulting in consensus genotypes from 13 polymorphic loci for statistical analysis (see Table 4.3).

Table 4.3 The 13 polymorphic microsatellite loci successfully genotyped (producing consensus genotypes), with final annealing temperatures used and characterisation in *N. hainanus* (across all samples).

Locus	**Annealing Temp.(°C)**	**Allele size range (*N. hainanus*)**	**Number of alleles**
D1S548	53	161-173	3
D2S367	54	138-156	5
D5S1457	54	110-118	3
D5S1470	50	192-204	4
D6S265	56;54	118-134	5
D7S817	56;54	130-148	6
D9S302	56;54	188-192	2
D17S804	54	145-161	3
D20S206	53	132-144	2
DQcar	53	86-104	4
DXS8043	56;54	190-196	3
DXYS156	58	115-125	2
HPRT1	56;54	138-148	3

Sex-determination

To investigate the present sex ratio, all samples from the current population were genotyped using a fluorescently-labelled 'Amelogenin' primer, which amplifies a region within the first intron of the X-Y homologous amelogenin gene containing a six bp deletion on the X homologue (Sullivan et al. 1993). As such, this primer amplifies both the X and Y homologues, yielding products with a six bp difference between them, thus permitting molecular identification of males (103 bp and 109 bp fragments in this study) and females (103 bp fragments only). Amelogenin was appropriate as the fragment lengths are relatively short, meaning amplification is viable for degraded DNA (Bradley et al. 2001). PCR amplification was conducted as previously described, using an annealing temperature of 55 °C. Human and gibbon controls were again included in all PCR replicates, and the Amelogenin primer was incorporated into a multiplex mix (where allele sizes in humans versus gibbon were obviously different for other primers) to ensure derived Amelogenin genotypes were those of gibbon samples and not human collectors. PCR replication and genotype scoring rules were applied as above to obtain consensus genotypes for each individual.

Data analysis

Preliminary analyses of microsatellite loci

To ensure the 13 genotyped polymorphic loci met the assumptions underlying the genetic diversity and population genetic parameters employed, genotyping errors due to false alleles, allelic dropout, stutter and null alleles were checked using MICRO-CHECKER V.2.2.3 (van Oosterhout et al. 2004). Null alleles can be detected as an excess of homozygotes, indicating loci deviating from Hardy-Weinberg Equilibrium (HWE), and must be discounted to allow discrimination of deviation caused by demographic processes of interest versus deviation caused by genotyping errors. LOSITAN (Antao et al. 2008) was used to detect any loci under selection by comparing observed differentiation, conditional on heterozygosity observed at each locus, against a simulated differentiation distribution under neutral expectations (Beaumont and Nichols 1996). I used 100,000 simulations and a confidence level of 0.95, such that loci falling outside the 95% confidence interval for neutral markers were identified as non-neutral and excluded from further analyses. Loci in linkage disequilibrium are non-randomly associated and therefore not statistically independent units, meaning they may bias estimates of allele and genotype frequencies (Huang et al. 2004) and must be excluded. Linkage disequilibrium between loci was tested in F-STAT V.2.9.3.2 (Goudet 2002) using Bonferonni correction (Rice 1989).

Genetic diversity

To quantify diversity, loci polymorphism was assessed by determining number of alleles/locus (*Na*), number of unique (private) alleles/locus (*Pa*), observed heterozygosity (H_o), and expected heterozygosity (H_e) for each locus for each population, and across loci for each population using F-STAT V.2.9.3.2 (Goudet 2002). Per-locus and overall allelic richness (*Ar*), along with private allelic richness (*Pr*), were calculated for each population using rarefaction (Kalinowski 2004) within HP-RARE V.1.1 (Kalinowski 2005), applying a minimum sample size (*n*) of seven diploid individuals (i.e. number of genes, '*g*'=14). Rarefaction allows comparison between unequal population samples by reducing the bias *n* can introduce in estimates of allelic richness; larger samples are more likely to contain more alleles and to capture rare alleles than smaller samples (Kalinowski 2005).

Differences in genetic diversity between current and historical populations, and any potential loss of genetic variation over time, were assessed by comparing *Na* and H_e. *Ar* is more sensitive to population bottleneck effects than other measures of genetic diversity when such measures are quantified using microsatellites, as alleles can be lost from such loci before heterozygosity changes (Spencer et al. 2000, Leberg 2002). Therefore, I also compared *Ar* (and *Pr*) between current and historical populations to determine if any decline was due to loss of alleles from the historical population. Parametric tests of statistical significance for such comparisons require sample sizes >2*g* to allow estimation of sampling variance (Kalinowski 2004). As samples were limited (less than 2*g* =28) for both populations, the non-parametric Wilcoxon signed-rank test was used to test for hypothesised declines within R V.2.15.1 (R-Core-Team 2012).

Inbreeding

The extent of inbreeding within current and historical populations was assessed by comparing H_e to H_o, and assessing the coefficient of inbreeding (F_{IS}) (Wright 1965, Weir and Cockerham 1984). F_{IS} measures the deviation of observed heterozygosity in a population from that expected under HWE. Populations that show significant negative or positive F_{IS} values deviate from HWE, which assumes random mating (F_{IS}=0). Inbreeding-driven deviations from HWE were evaluated by estimating F_{IS} for each locus and across all loci for each population using F-STAT V.2.9.3.2 (Goudet 2002) with Bonferroni correction (Rice 1989).

Genetic differentiation

The extent of genetic differentiation, and thus genetic shift, between current and historical populations was examined via three standard approaches. I estimated the fixation index, F_{ST} (Wright 1965, Weir and Cockerham 1984, Cockerham and Weir 1993), which measures differentiation by comparing mean reduction in heterozygosity due to genetic drift among populations. Higher values indicate higher degrees of differentiation, with a theoretical maximum of 1.0 indicating that populations are fixed for different alleles, and a minimum of 0.0 indicating no differentiation (Wright 1965). Pairwise F_{ST} (Cockerham and Weir 1993) was calculated using F-STAT V.2.9.3.2 , with a randomisation approach to test for significance (Goudet 2002). Jost's estimator of actual population differentiation D_{est} (Jost 2008) was also calculated using SMOGD V.1.2.5 (Crawford 2010), with bootstrapping over 1,000 replicates. D_{est} measures differentiation by partitioning heterozygosity into within and between population components and is thought to be more reliable than F_{ST} when characterising differentiation using markers with high mutation rates, like microsatellites, as F_{ST} estimates can decline with increasing polymorphism (Jost 2008).

To graphically assess any pattern of differentiation and distinguish any clustering of historical and modern samples, I conducted Principal Coordinates Analysis (PCoA) using pairwise genetic distances between all samples within GenAlEx V.6.5 (Peakall and Smouse 2006). PCoA condenses genotype information from multiple loci into a single matrix of genetic distances between each pair of samples using eigenvectors, and distinguishes the main axes explaining the greatest variation in this matrix by producing a set of coordinates on a number of axes. The resultant plot provides a spatial representation of the genetic distances (dissimilarity) between samples, allowing patterns of association, or separation, among individuals (from both populations) to be identified.

Thirdly, I used a Bayesian clustering approach implemented within STRUCTURE V.2.3.4 (Pritchard et al. 2000) to evaluate evidence of population structure. The model uses multi-locus genotype data to assign individuals to populations without any prior information on population distinction. Using 100,000 iterations, following a burn-in period of 10,000 iterations, I assessed the extent of partitioning by exploring a range of values for the number of populations prior, '*K*', with five replicates per *K* value (*K*=1-8). As the historical population is, to some extent, ancestral to the current population, an admixture model and independent allele frequencies were adopted, as appropriate for closely related populations, but where allele frequencies can be expected to be reasonably different (Pritchard et al. 2000). Optimal *K* was determined using the ΔK approach (Evanno et al. 2005) implemented in STRUCTURE HARVESTER V.0.6.93 (Earl and vonHoldt 2012). This method tracks rate of change in log probability between successive *K* values to detect a peak in change corresponding to the optimal value of *K*.

Genetic bottleneck

Evidence of a genetic bottleneck was assessed graphically by investigating a potential shift in the mode of allele frequencies (Luikart et al. 1998). In a non-bottlenecked population, a large number of alleles are expected to occur in low frequencies for polymorphic, selectively-neutral loci (Chakraborty et al. 1980), producing an 'L-shaped' allele frequency distribution. However, when a population suffers a bottleneck, rare alleles are lost rapidly, meaning more alleles occur at intermediate and high frequencies and the mode allele frequency shifts to the right (Luikart et al. 1998). Evidence of a shift in mode allele frequency between historical and current populations was assessed by grouping alleles across polymorphic loci for each population into 10 frequency classes (0.001–0.100, 0.101–0.200 etc. up to 1.0). The resultant histograms and mode allele frequencies were then compared.

A second, quantitative assessment evaluated 'heterozygosity excess' – greater than expected heterozygosity from the observed number of alleles, for a significantly higher proportion of loci than predicted under a given mutation model. Alleles are lost by chance at neutral loci through genetic drift in all populations, but this is balanced by mutations producing new alleles in a pattern known as 'mutation-drift equilibrium' (Hartl and Clark 1989). In bottlenecked populations, loss of alleles occurs faster than loss of heterozygosity, causing a transient deficiency in the number of alleles but maintenance of heterozygosity, producing a heterozygosity excess (Luikart et al. 1998). This excess lasts for up to 250 generations, thus persisting as a signature of a bottleneck during this period, after which heterozygosity also declines. Heterozygosity excess was tested using BOTTLENECK V.1.2.02 (Cornuet and Luikart 1996), under four mutation models, using three significance tests (sign, standardised differences, Wilcoxon sign-rank). The infinite allele mutation (IAM) model assumes each new mutation can produce any new allele, while the stepwise mutation model (SMM) assumes mutations produce alleles that are one step (repeat unit) different to the original allele (Cornuet and Luikart 1996). Microsatellites, however, rarely confirm strictly to either of these models, so a two-phase model (TPM) accommodating both types of mutation may be more appropriate (Piry et al. 1999). Therefore, I adopted the IAM, SMM, and two TPM variants with 70% and 90% SMM (thus 30% and 10% IAM).

Effective population size

Effective population size (N_e) was estimated for both current and historical populations using a number of standard 'single-sample' approaches: linkage disequilibrium, heterozygosity excess, and molecular coancestry within NeEstimator V.2.0 (Do et al. 2013), and full-likelihood sib-ship assignment, as described by Wang (2009), within COLONY V.2.0.4.5 (Jones and Wang 2010). Single-sample approaches are advantageous as they require only one population sample, but they may be less precise than 'temporal methods', which utilise samples over multiple generations (Waples 1989). Therefore, I also used a Bayesian approach implemented in TMVP (Beaumont 2003). This approach samples independent genealogical histories from temporally-spaced gene frequency data (all samples, pooled) to give a posterior distribution of estimated 'historical N_e' (at the time of the oldest historical sample) and 'current N_e' (at the time of the most recent sample). It is therefore possible to detect a change in N_e over the sample period (1899-2011), and thus uncover additional evidence of a bottleneck. The analysis assumes that the sampling period is sufficiently short that any mutation effects can be ignored, and accommodates unequal samples sizes across loci. Allele frequencies were calculated for each temporally-spaced sample (utilising museum specimen collection dates), with time measured in generations since a sample was taken (until $t=0$ for the most recent). I specified an average gibbon generation time of 15 years (Chivers et al. 2013) to distinguish temporal samples, and a rectangular prior of (0,2000) for both historical and current N_e. I determined the joint mode of the posterior distribution of historical and current N_e estimates, discarding the first ten estimates (0.5%) of the simulated chain as burn-in, and applying a smoothing parameter of α=0.6 (after exploring α=0.3-0.7) within R V.3.0.1 (R-Core-Team 2013). This α-value was subsequently employed to determine the 95% higher posterior density (HPD) limits of each N_e, as it produced a sharp joint mode that was not at the upper limit of the priors for either N_e.

Relatedness of individuals in the current population

Relationships between individuals in the current population were investigated using COLONY V.2.0.4.5 (Jones and Wang 2010), which infers parentage and sibling-relationships (full and half sib-ships) jointly over the entire population to determine the best configuration of relationships between individuals under maximum likelihood (ML). The most likely mothers and fathers are identified from specified candidate adult males and females, and where the likely parent of an offspring is not found among candidates, the program infers a probable father or mother based on observed offspring genotypes. Therefore, information on likely sib-ships between sampled individuals is revealed, even when the parents of the individuals are not sampled. All sampled mature males and females were included as candidate parents, regardless of current social group affiliations. Known relationships (known mothers, and known paternal exclusions) were incorporated where sufficient demographic data were available (from long-term observations; BNNR Management Office pers. comm., July 2011). An arbitrary genotyping error rate of 0.01 was imposed, as error was assumed to be low due to the conservative genotyping approach adopted, and 50% probability that an actual father or mother of an offspring was included in the candidate datasets was employed. Inbreeding was incorporated into the model but did not alter the configuration produced. The resultant ML configuration was used to construct a pedigree for the current population within Pedigree Viewer V.6.5B (Kinghorn and Kinghorn 2010).

The coefficient of relatedness (*r*) between individuals was also determined using ML-RELATE (Kalinowski et al. 2006). This method adopts a ML algorithm to estimate relatedness coefficients, which is generally more accurate than other estimators under various sampling conditions (Milligan 2003). Pairwise relatedness between all individuals was estimated. ML *r* estimates, together with the ML configuration, therefore indicated the degree and structure of relatedness within the current population over more than one generation to reveal the probable shared parentages which may have produced the observed relatedness/relationships. To further inform this analysis, I also re-ran the COLONY and ML-RELATE analyses incorporating the two most recently-collected museum specimens (BWL 671 and BWL 672) from the historical population. These specimens were collected from the Bawangling area in the 1980s. The eldest individual in the current population (B1) is estimated to be anywhere up to 45 years old (Li et al. 2010), and therefore may be of the same cohort as these specimens, making it informative to assess relatedness between these samples and the current population.

Sex ratio

Based upon sex-determination revealed by the Amelogenin consensus genotypes, I calculated the sex ratio of: i) all individuals sampled from the current population; ii) all individuals in Group B; and iii) offspring within Group B. The latter represents an estimate of the sex ratio of the remaining population's immature offspring (as not all offspring could be sampled) and the ratio with greatest implications for population viability. To ascertain if the observed ratios indicate any bias attributable to effects of small population size, I tested each ratio against Pearson's Chi-squared statistic (χ^2) for significant deviation from a 1:1 ratio of males to females, as would be expected by chance. I applied Yate's correction (Yates 1934) to prevent incorrect detection of statistical significance due to small sample sizes.

Results

Genotyping success

Extractions from all sampled individuals from the current population successfully amplified, producing consensus genotypes for all 13 loci genotyped. For historical samples, only DNA extracted from eight museum specimens amplified successfully, and two of these samples (NHM 1911, BWL 1980 (672)) failed to amplify for two loci each, despite replicate PCRs (Table 4.4). The small size of the historical sample (n=8) precluded further temporal divisions, therefore historical samples were pooled into one historical 'population' for all analyses. Although this may limit the inferences of the analyses, comparing metrics of genetic diversity generated from a modern population sample and a pool of historical samples from an extended temporal period is common in studies of decline in genetic diversity (Gottelli et al. 2004, Holbrook et al. 2012).

Preliminary analyses of microsatellite loci

No significant homozygote excess was detected for any loci (P>0.05 for all loci) indicating no evidence of null alleles. There was also no evidence of allelic dropout or scoring error due to stutter. Simulation results from LOSITAN identified two loci that fell outside the 95% quantile for neutral markers: D17S804 and D20S206 both fell above the 95% confidence interval, indicating they were candidates for positive selection (Figure 4.1). All other markers were within neutral expectations. Genotype data for D17S804 and D20S206 were therefore excluded from further analyses. Among the remaining 11 neutral polymorphic loci, there was no evidence of significant linkage disequilibrium between any pairs of loci for either population (all P-values>0.0005, adjusted 5% P-value). All subsequent analyses therefore utilised genotypes from these 11 loci.

Table 4.4 Number of supporting replicates per locus used to produce consensus genotypes for each current and historical sample (from indicated number of faecal samples and DNA extractions) for 13 polymorphic loci successfully genotyped.

Hainan gibbon samples		**Loci genotyped**												
Current samples (*n*=9)		**D1S548**	**D2S367**	**D5S1457**	**D5S1470**	**D6S265**	**D7S817**	**D9S302**	**D17S804**	**D20S206**	**DQcar**	**DXS8043**	**DXYS156**	**HPRT1**
A	1 sample, 4 extractions	10	12	11	10	10	13	10	15	12	17	10	13	11
B1	2 samples, 6 extractions	23	30	24	23	27	24	20	30	25	28	24	28	27
B2	4 samples, 8 extractions	27	35	33	27	32	24	27	32	30	30	34	36	30
B3	3 samples, 8 extractions	28	26	26	23	24	24	23	25	23	25	23	26	25
B4	2 samples, 5 extractions	12	16	15	12	13	13	14	15	12	13	12	15	15
B5	2 samples, 4 extractions	12	16	15	11	12	12	15	17	12	12	14	14	12
B6	1 sample, 5 extractions	12	18	16	15	14	15	17	20	15	15	14	18	18
B7	2 samples, 8 extractions	34	38	36	35	33	37	38	38	36	34	35	38	34
C	1 sample, 3 extractions	10	13	10	13	13	12	14	15	12	12	12	15	14
Historical samples (*n*=8)		**D1S548**	**D2S367**	**D5S1457**	**D5S1470**	**D6S265**	**D7S817**	**D9S302**	**D17S804**	**D20S206**	**DQcar**	**DXS8043**	**DXYS156**	**HPRT1**
DUB 1899	1 sample, 1 extraction	5	5	5	5	5	5	5	5	5	5	5	5	5
BER 1909	1 sample, 1 extraction	5	5	5	5	5	5	5	5	5	5	5	5	5
NHM 1911	1 sample, 1 extraction	5	5	5	5	5	5	none	5	5	5	5	none	5
SCIEA 1964 (0502)	1 sample, 1 extraction	5	5	5	5	5	5	5	5	5	5	5	5	5
SCIEA 1964 (0503)	2 samples, 2 extractions	10	10	10	8	8	10	8	10	10	10	9	10	9
SCIEA 1960	2 samples, 2 extractions	10	10	10	8	10	10	7	10	10	10	8	10	10
BWL 1980 (671)	2 samples, 2 extractions	10	10	10	10	10	10	10	10	10	10	10	10	10
BWL 1980 (672)	1 sample, 1 extraction	5	5	5	5	5	5	5	5	5	5	none	5	none

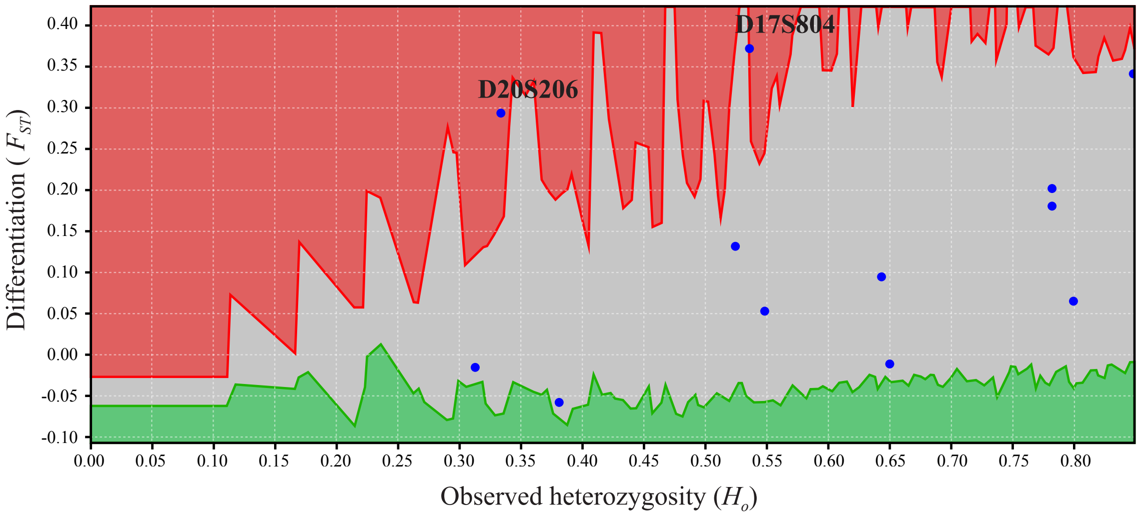


Figure 4.1 LOSITAN selection test for polymorphic microsatellite loci; observed differentiation (F_{ST}) is plotted as a function of observed heterozygosity (H_o) for each loci (blue dots). The light grey area corresponds to differentiation simulated under neutral expectations: loci within this area are within 95% confidence interval for neutral loci; markers above (in red area) are candidates for positive selection, and those below (in green area) are candidates for balancing selection.

Genetic diversity

The genetic diversity of both the current and historical populations was found to be low, with small *Na* and *Ar* values observed for each locus and across all loci for each population, indicating a low level of polymorphism for all loci in each population (Table 4.5). Despite this, the genetic diversity of the current population was lower still than that of the historical population for all metrics of diversity (Table 4.5). Across all loci, *Na* significantly declined by 32% from the historical to the current population (one-sided Wilcoxon W = 99.5, P<0.01), *Ar* significantly declined by 32% (one-sided Wilcoxon W = 103 P<0.01), and H_e significantly declined by 31% (one-sided Wilcoxon W = 97, P<0.01). For seven of the 11 loci (63%), alleles were found in the historical population that were missing from the current population (e.g. see Figure 4.2). This was confirmed by the significantly lower *Pr* in the current population (one-sided Wilcoxon W = 93, P<0.05), indicating 'historical' alleles have been lost over time and have not replaced by newly mutated alleles.

Inbreeding

For the current population, H_o was generally greater than H_e at each locus (nine of 11 loci; 81.8%), producing an overall trend of mean H_o greater than mean H_e (Table 4.5). The opposite was true of the historical population (H_e>H_o for eight of 11 loci; 72.7%). However, despite these trends, after Bonferroni correction, none of the estimated F_{IS} values proved to be

Table 4.5 Genetic diversity for each neutral, polymorphic microsatellite locus and summary statistics (overall mean or total plus S.E.) of the genetic diversity of current and historical populations across all loci. Diversity measures are: number of alleles/locus (*Na*); number of unique (private) alleles/locus (*Pa*); allelic richness (*Ar*); private allelic richness (*Pr*); observed heterozygosity (H_o); expected heterozygosity (H_e). The inbreeding estimator (F_{IS}) was used to detect deviations from HWE for each locus and each population. Overall values (in **bold**) represent population values: average *Na*, *Pa*, *Ar*, *Pr*, H_o, H_e, and overall F_{IS}.

Locus	**Historical population (*n*=8)**							**Current population (*n*=9)**						
	Na	*Pa*	*Ar*	*Pr*	H_o	H_e	F_{IS}	*Na*	*Pa*	*Ar*	*Pr*	H_o	H_e	F_{IS}
D7S817	5	4	4.750	4.00	0.625	0.750	0.176	2	1	2.000	1.00	1.00	0.529	-1.00
DQCar	4	2	3.867	2.00	0.750	0.592	-0.292	2	0	2.000	0.008	0.889	0.523	-0.778
D1S548	3	0	3.00	0	0.875	0.692	-0.289	3	0	2.961	0	0.778	0.621	-0.273
HPRT1	3	1	3.00	1.00	0.286	0.670	0.593	2	0	2.000	0	0.222	0.366	0.407
D9S302	2	0	2.00	0	0.286	0.440	0.368	2	0	2.000	0	0.222	0.366	0.407
DXYS156	2	0	2.00	0	0.857	0.527	-0.714	2	0	1.778	0	0.111	0.111	0.00
D5S1470	3	2	3.00	2.00	0.571	0.615	0.077	2	1	1.995	0.995	0.333	0.294	-0.143
DXS8043	3	1	3.00	1.00	0.429	0.692	0.400	2	0	2.000	0	0.444	0.471	0.059
D6S265	5	1	4.867	1.00	0.500	0.767	0.364	4	0	3.956	0.125	1.00	0.725	-0.412
D2S367	4	3	3.875	3.00	0.500	0.717	0.317	2	1	2.000	1.00	1.00	0.529	-1.00
D5S1457	3	1	2.875	1.00	0.375	0.425	0.125	2	0	1.961	0	0.222	0.209	-0.067
Overall	**3.364**	**1.364**	**3.290**	**1.340**	**0.550**	**0.626**	**0.129**	**2.273**	**0.273**	**2.240**	**0.280**	**0.566**	**0.431**	**-0.337**
S.E.	0.310	0.388	0.288	0.358	0.063	0.036	n/a	0.195	0.141	0.194	0.139	0.111	0.055	n/a

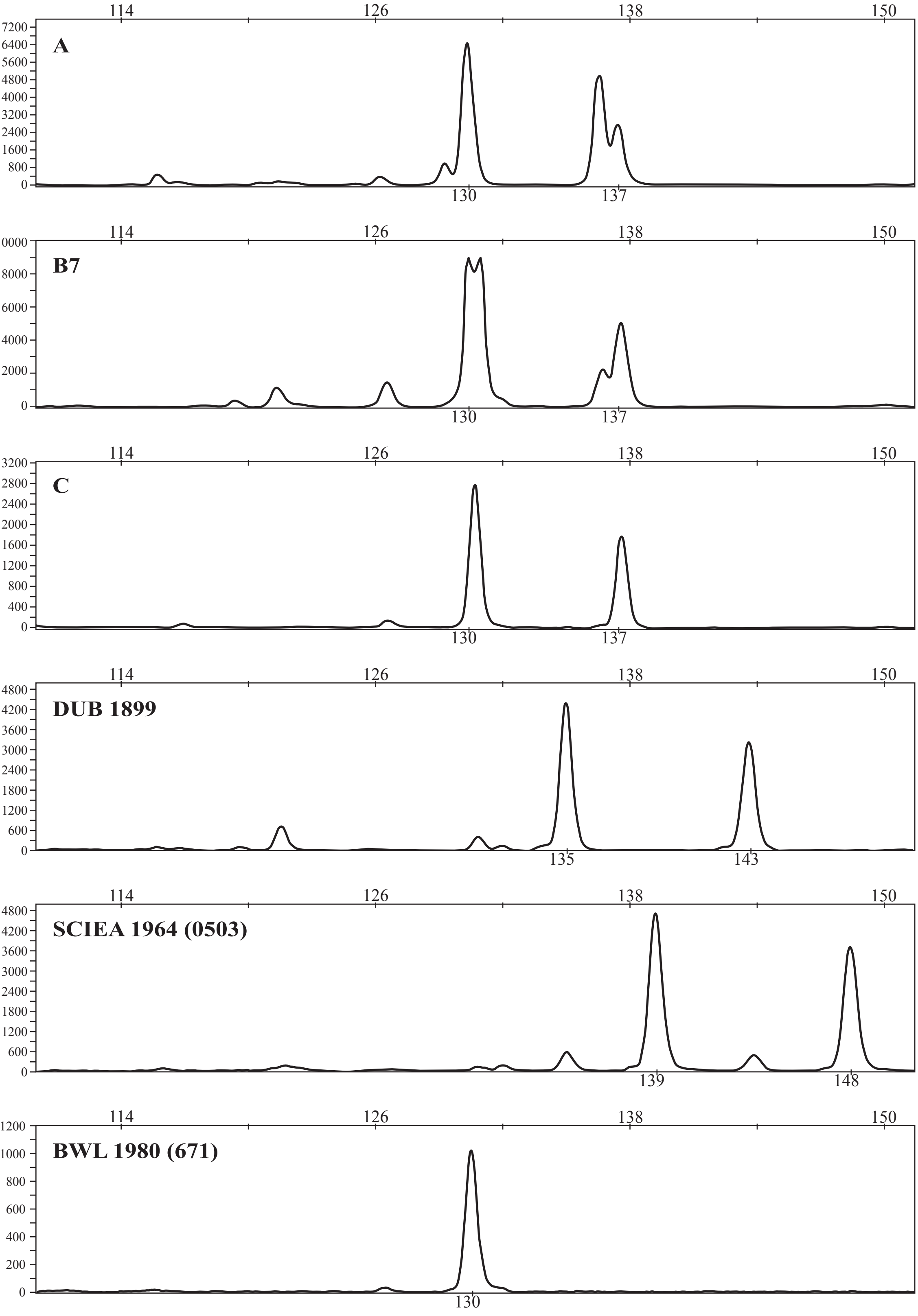


Figure 4.2 Electropherogram of microsatellite locus D7S817 (output from GeneMapper V.4.1, Applied Biosystems) showing unique allele sizes for a selection of current (A, B7, C) and historical (DUB 1899, SCIEA 1964 (0503), BWL 1980 (671)) samples. Alleles of 135, 139, 143, 148 bp were found only in historical samples, 130 bp allele was found in both the current and historical samples, and 137 bp allele was found only in the current population.

significant for any locus in either population, or overall for either population (all P-values >0.002, adjusted 5% P-value). Neither any individual loci, nor the current or historical populations overall, therefore significantly deviated from HWE based upon F_{IS}.

Genetic differentiation

Current and historical populations showed significant population differentiation (pairwise F_{ST} = 0.156, $P<0.05$), indicating that of the total genetic variation observed across both populations, 15% is distributed between populations and 85% is found within populations. Jost's estimator of actual differentiation was of a similar, but slightly smaller magnitude (D_{est} across all loci = 0.100). Together these indices suggest substantial divergence of the current population from the historical due to genetic drift. PCoA confirmed temporal differentiation between current and historical populations, and revealed additional nuances of divergence. The first two PCoA axes explained 28.30% and 18.12% respectively of the total genetic variation captured across all samples (Figure 4.3). Current population samples clustered along the second axis (as demarcated by the dashed oval), indicating little difference and thus little genetic variation, but dispersed slightly along the first axis. This dispersion consisted most notably of individuals from Groups A and C, along with the eldest individual in the current population (B1) separating slightly from the remaining individuals of Group B. Historical samples dispersed along both axes and only clustered loosely, away from current samples, indicating greater genetic variation compared to the current population, reduction in genetic diversity over time and divergence between current and historical populations.

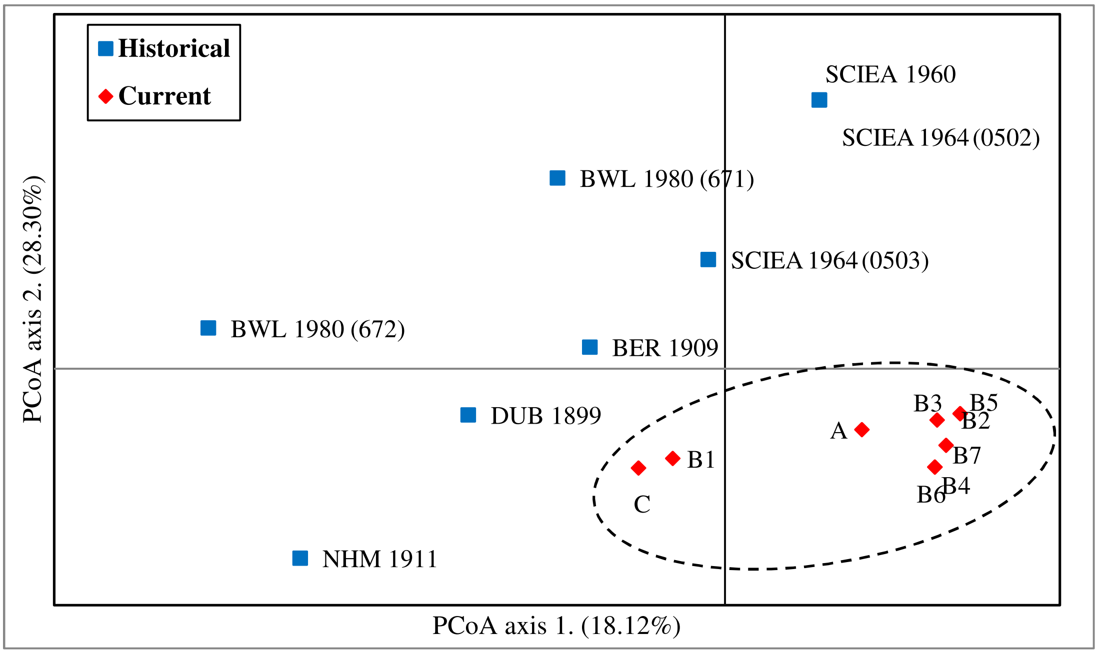


Figure 4.3 Principal Coordinate Analysis (PCoA) based on pairwise genetic distances between all historical (squares) and current (diamonds) samples. Proportion of total variance explained by each axis was 28.30% for axis 1 and 18.12% for axis 2. The dashed oval encircles current population samples.

Bayesian clustering analysis distinguished three genetic populations, with the peak in ΔK corresponding to K=3 clusters (Figure 4.4). Ninety five percent of current population samples fell into one cluster, indicating differentiation of this population from the historical samples (Figure 4.5). Historical samples subdivided into two genetic populations (47.2% and 49.2%) corresponding roughly to a split between very old samples (1899-1911) and more recent samples (1960s-1980s), although one sample from the 1980s (BWL672) clustered more often with older historical samples. This clustering is likely due to this sample retaining some of the 'older' alleles, i.e. those present in the very old samples, or may be the result of missing data (this sample failed to successfully amplify for two loci). Approximately 3.5% of current samples (corresponding to a small proportion of two samples) were clustered with one of the two historical genetic populations, indicating these samples therefore likely retain a small number of 'historical' alleles present in historical samples/populations. Regardless, clustering revealed genetic differentiation between current population and historical samples, whether the latter are considered as one, or two populations.

Genetic bottleneck

The historical population exhibited the L-shaped allele frequency distribution expected in non-bottlenecked populations, with a large number of alleles falling into lower frequency classes (0.001-0.2) and few alleles falling into intermediate (0.201-0.8) and higher (0.801-1.0) frequency classes (Figure 4.6). The current population showed fewer alleles in low frequency classes and more alleles in intermediate and higher frequency classes. Mode allele frequency across all loci in the historical population was 0.188, but for the current population the mode was higher at 0.5, indicating a modal shift to the right, as evident in the histograms.

For the current population, all three significance tests indicated significant heterozygosity excess under the IAM model, and two of the three tests indicated significant excess under the more conservative TPM with 70% SMM (Table 4.6). There was no evidence of heterozygosity excess under the SMM model for this population. As fewer than 20 loci were genotyped, results from the strict SMM model may be less reliable. The TPM with 90% SMM indicated heterozygosity excess in the current population from the Wilcoxon test only. Significant heterozygosity excess was also revealed within the historical population for two of the three tests under the IAM model and TPM with 70% SMM, and from the Wilcoxon test under the TPM with 90% SMM, but again no significant excess was detected under the SMM model. Results of standardised differences tests for both populations and all models should however be treated with caution, as the test statistic (T2) only approaches a Gaussian normal distribution if the number of loci used is large (>20 loci) (Cornuet and Luikart 1996). The non-parametric Wilcoxon test is the most powerful and robust test when few polymorphic loci are used (Piry et al. 1999), so results of this test can be taken as evidence of a bottleneck in both current and historical populations.

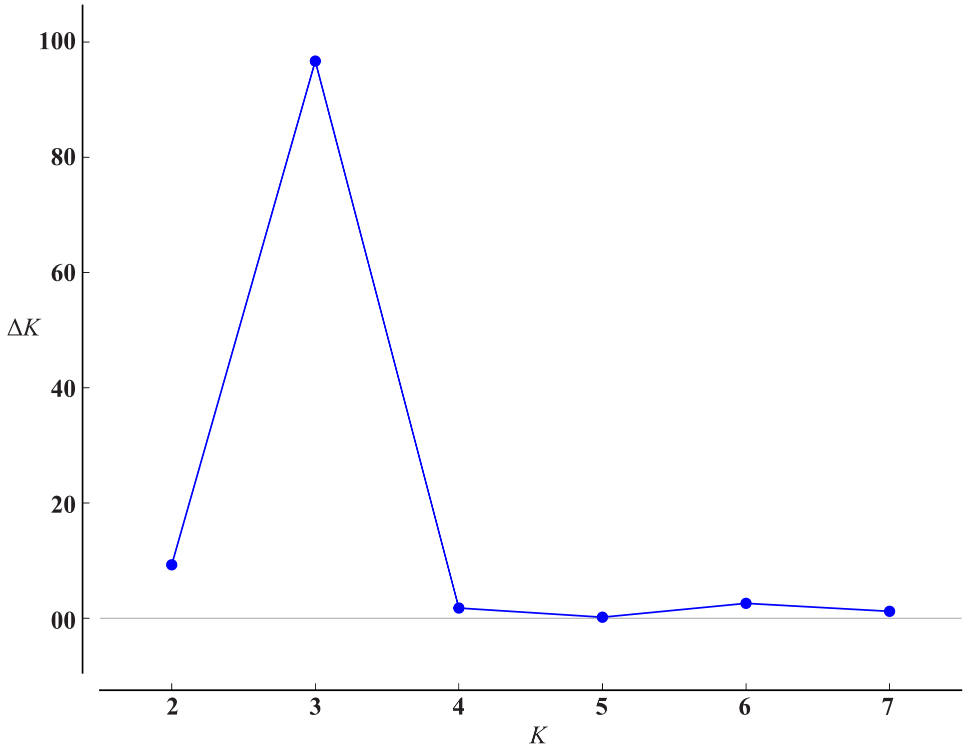


Figure 4.4 Second order rate of change of likelihood function with respect to *K* (Δ*K*) over successive *K* values, following Evanno et al. (2005). The peak indicates the modal value of Δ*K* distribution corresponding to optimal *K* (i.e. most likely level of population structure).

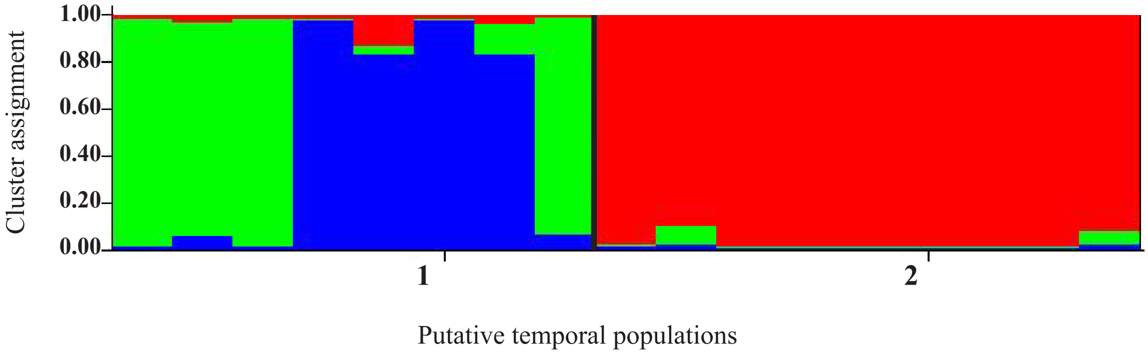


Figure 4.5 Population assignment of all samples (current and historical) by STRUCTURE (Bayesian clustering analysis) into three genetically distinct populations (clusters, *K*=3) shown as green, blue and red. Each individual is represented as a separate vertical bar sectioned into coloured segments representing the different genetic populations. The length of the segment is proportional to the likelihood of assignment (proportion of times in 100,000 iterations) of the individual to that population. Putative temporal populations are shown as 1=historical, 2=current separated by a black line, although this information was not used *a priori* within the analysis.

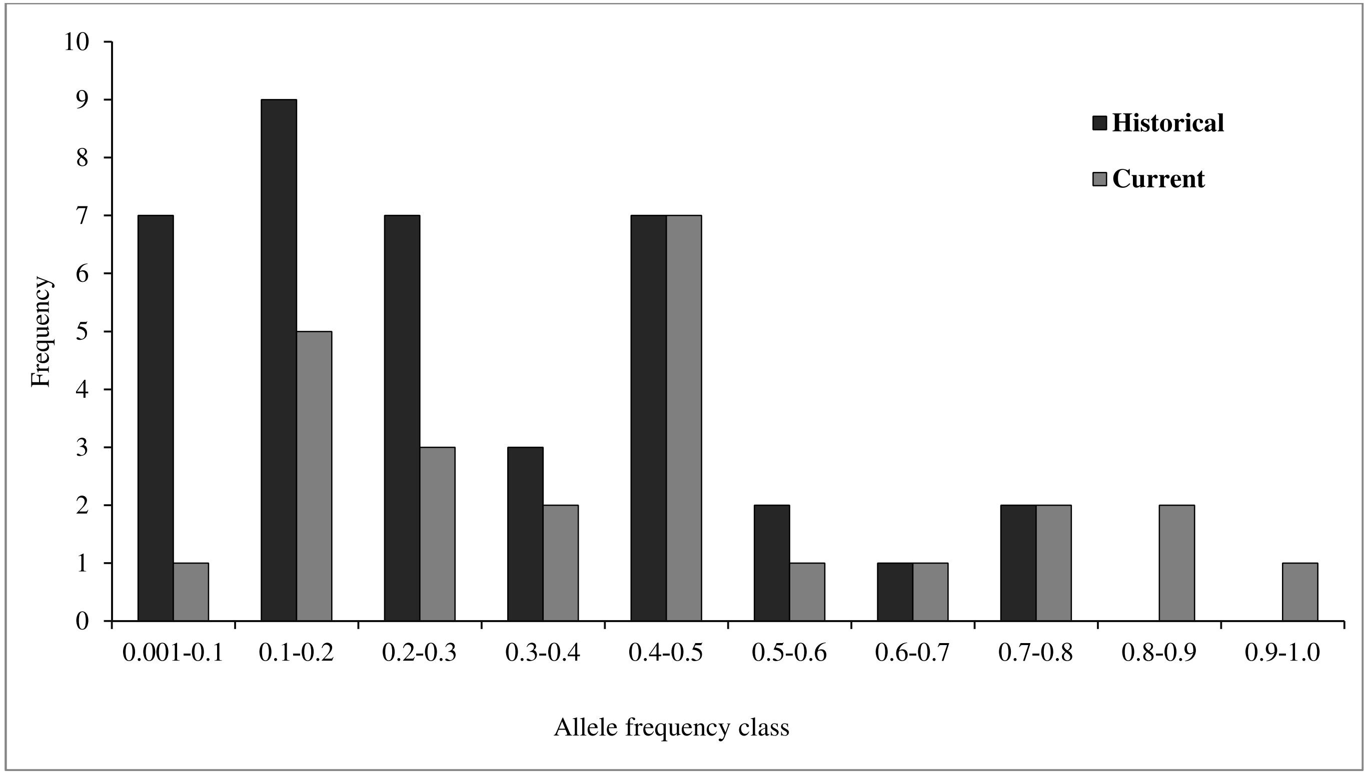


Figure 4.6 Distribution of allele frequencies for historical and current populations across all loci. Historical and current frequencies across classes shown as dark and light grey columns respectively.

Table 4.6 Results from heterozygosity excess tests in BOTTLENECK using three significance tests and four models of allele mutation (IAM, SMM, and two TPM variants). Significant *P*-values (<0.05) are indicated in **bold**.

Test	**Test statistic/probability variant**	**Historical population**				**Current population**			
		IAM	**SMM**	**TPM (70% SMM)**	**TPM (90% SMM)**	**IAM**	**SMM**	**TPM (70% SMM)**	**TPM (90% SMM)**
Sign test	Expected number loci with heterozygosity excess	6.16	6.50	6.36	6.60	5.66	5.72	5.29	5.56
	Observed number loci with heterozygosity excess	9	8	9	9	9	8	8	8
	Probability (*P*-value)	0.073	0.274	0.092	0.118	**0.040**	0.140	0.090	0.119
Standardised differences test	T2	2.65	1.15	1.92	1.54	2.32	1.37	1.75	1.54
	Probability (*P*-value)	**0.0040**	0.124	**0.028**	0.062	**0.010**	0.086	**0.040**	0.061
Wilcoxon sign-rank test	Probability (one tail for heterozygosity deficiency)	0.999	0.926	0.992	0.966	0.994	0.913	0.966	0.966
	Probability (one tail for heterozygosity excess)	**0.001**	0.087	**0.011**	**0.042**	**0.008**	0.103	**0.042**	**0.042**
	Probability (two tails for heterozygosity excess or deficiency)	**0.002**	0.175	**0.021**	0.083	**0.016**	0.206	0.083	0.083

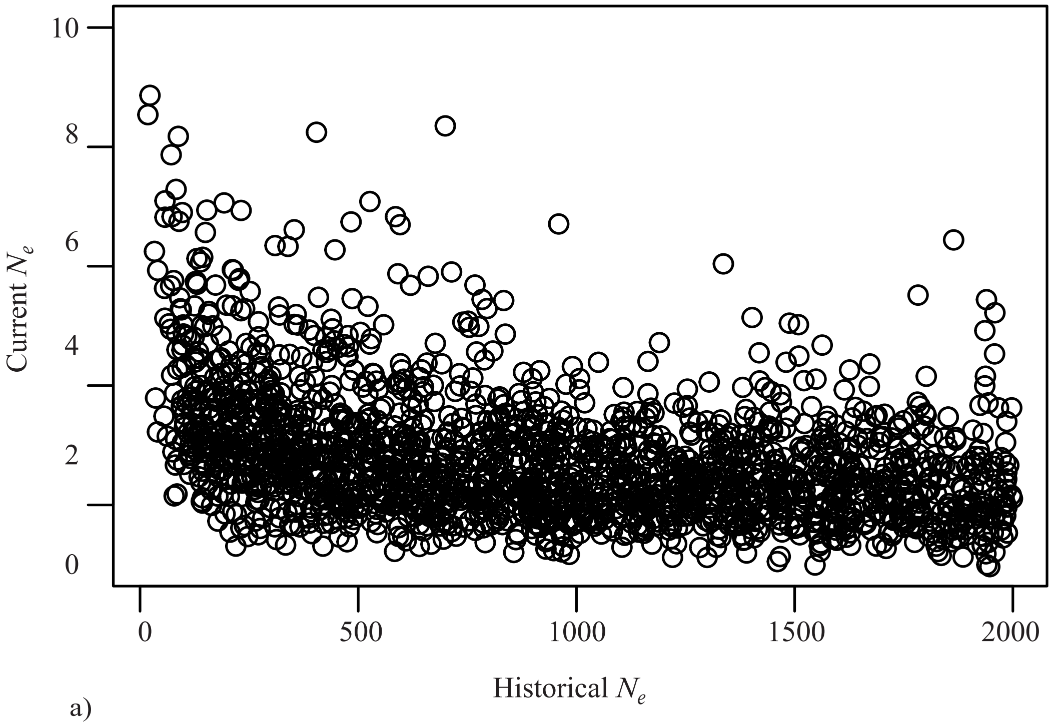
Effective population size

All single-sample estimates of N_e reported exceptionally low effective population size for the current population (Table 4.7). There was substantial variation in values of historical N_e, but a trend for a slightly larger N_e for the historical population. However, large confidence intervals for all estimates limit comparison between the temporal populations. The apparent lack of difference in historical versus current N_e implied by these estimates and confidence intervals is ambiguous: it could result from limitations of the single-sample approaches for small n, or may represent a stable, low N_e over time that would pre-date the precipitous decline of the species in the mid-20th century. Accuracy of the single-sample N_e estimates derived here is likely limited, and at best, these estimates are approximations of true N_e.

Bayesian estimation of N_e at the time of the oldest and most recent samples indicated temporal change in N_e (Figure 4.7a). The density of points in the posterior distribution is proportional to the probability density of historical and current N_e, and the off-diagonal distribution of points indicates that current N_e is not equal to historical N_e. The exceptionally flat posterior distribution, with points densely concentrated along the x-axis (historical N_e), provides strong evidence of a recent decline in N_e between the time of the oldest historical sample (1899) and the current population (2011). This also indicates that current N_e is very low. The joint mode (and 95% higher posterior density, HPD limits) for the marginal from the density estimation is: historical N_e=993.56 (95% HPD limits: 75.47–1912.04) and current N_e=2.15 (95% HPD limits: 1.15–5.02) (Figure 4.7b). Estimation of the mode of the historical N_e is somewhat uncertain, indicated by the larger 95% HPD limit range, but regardless, there is strong evidence that the species' effective population size was certainly larger at the start of the 20th century than it is today.

Table 4.7 Estimates of effective population size (N_e) of current and historical populations inferred via linkage disequilibrium (LD), heterozygosity excess (HE), molecular coancestry (Coancestry), and full-likelihood sib-ship assignment (Full likelihood) methods, with 95% confidence intervals.

Population	**LD**	**95% CI**	**HE**	**95% CI**	**Coancestry**	**95% CI**	**Full likelihood**	**95% CI**
Historical	2.8	1.5-16.5	infinity	8.5-infinity	4.4	2.1-7.6	16	7.0-86
Current	3.1	1.2-infinity	2.6	1.4-infinity	1.8	1.0-2.9	4	2.0-20



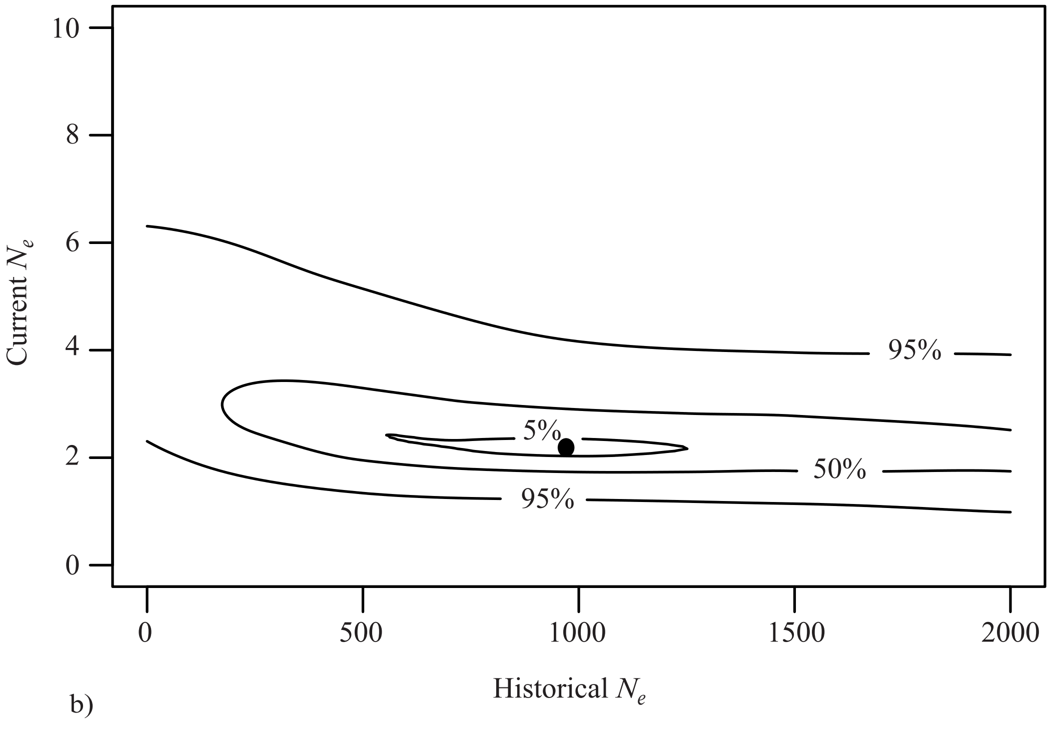


Figure 4.7 Bayesian estimates of 'historical N_e' and 'current N_e' following the TMVP method of Beaumont (2003): a) posterior distribution of historical and current N_e with the density of points being proportional to the probability density of N_e at the time of the oldest and most recent samples; b) 5%, 50% and 95% higher posterior density limits of the posterior distribution, and joint mode of historical and current N_e (plotted as a single solid circle).

Relatedness of individuals in the current population

The ML configuration of relationships, displayed in the pedigree (Figure 4.8), revealed both direct relationships between sampled individuals and relationships inferred through shared genotypes (deduced via theoretical parents–represented as starred and dashed numbers). Known Group B parent-offspring associations incorporated *a priori* were replicated (including maternity of B4-B7 assigned to B2, and B2 assigned to B1). Additional relationships within Group B were revealed, including those implied by field observations but not included *a priori* due to limited data, e.g. male B3 was assigned paternity of B7. Paternities of older Group B offspring (B4, B5, B6) were not assigned to B3, but to another theoretical male (*2). This may reflect a sampling limitation or true change in breeding male of Group B between conception of B6 and B7, for which there is anecdotal field evidence (BNNR Management Office pers. comm., June 2011). This theoretical male was also allocated paternities of the current Group B breeding pair (B2 and B3), which would indicate inbreeding within the group: B2 mating with her own father to produce B4-B6; B2 and B3 as siblings producing B7. There is, however, no direct observational evidence to support this inference.

ML pairwise r estimates supported many of these Group B relationships (Table 4.8). Full-sibling relationships between Group B offspring (B4-B7) were evident ($r \geq 0.5$ for each pairwise comparison of these individuals), except for B5 and B7 which was slightly lower ($r=0.32$), but still greater than half-sibship. Parent-offspring level relationships were supported between B2 and her known offspring, B4-B6 ($r \geq 0.5$), except B7 ($r=0.32$), which is still greater than half-sibship. Similarly, pairwise coefficients between B3 and Group B offspring supported parent-offspring relationships ($r \geq 0.5$), except for B5, which was closer to the half-sib level ($r=0.27$).

Overall, the ML r estimates indicated a high level of relatedness between all individuals in the remaining Hainan gibbon population. Average relatedness across the sampled population was relatively high, roughly between half- and full-sibs (mean $r=0.34\pm0.05$). The average level of relatedness within Group B was approximately full-sibs or parent-offspring (mean $r=0.45\pm0.07$). Between social group relatedness was slightly lower, as expected, between the level of cousins and half-sibs. The relatedness of Groups B and C (mean $r=0.18\pm0.09$) was similar to that of Groups B and A (mean $r=0.16\pm0.07$), approximately at the level of cousins, while the relatedness of Groups A and C was slightly higher ($r=0.38$, no S.E. as comparison between two individuals only), at least half or almost full-sibs. Relationships between individuals in social groups were also revealed. A maternal half-sib relationship was inferred between B3 and the adult male sampled from Group A (by #1; Figure 4.8), although ML pairwise r supported a closer, full-sib relationship ($r=0.5$). Adult males from Groups A and C were revealed as paternal half-sibs (by *1), or closer, with $r=0.38$ supporting between full and half-sibs. The oldest female in the population, B1, was allocated maternity of the adult male sampled from Group C, with $r>0.5$ supporting a parent-offspring relationship between these individuals.

Further analysis revealed possible historical relationships. When the two most recent historical samples (BWL 671 and 672, c. 1980s) were incorporated, both the ML configuration (Figure 4.9) and ML r estimate (Table 4.8; $r=0.17$) indicated a roughly half-sib relationship between one of these historical individuals (BWL 672) and the oldest individual of the current population (B1). The pedigree indicated this may have been the result of a shared mother (#2). There was also limited evidence for an affiliation between BWL and the Group C adult male ($r=0.13$, approximately cousins), although this was not supported by the ML configuration. The two historical individuals appear to have been between full and half-sibs ($r=0.35$), likely the result of a shared father (*3). All relationships observed for the current population under the original configuration were preserved.

Sex ratio

Amelogenin consensus genotypes were obtained for all sampled individuals of the current population, allowing every individual to be sexed molecularly (Table 4.9). In all cases where sex of an individual was known *a priori*, inferred by direct observation of mature adults in the population, the Amelogenin genotypes confirmed the sex of these individuals. The sex-determination genotypes indicated the overall sex ratio in the sampled population to be two males for every female (Table 4.10). Within social Group B only, the ratio was closer to even proportions, with three females to four males. For the immature offspring in Group B, for which all sexes were previously unknown, the sex-determination genotypes revealed one female and three male offspring. This would suggest a strong male-biased sex ratio of offspring within the remaining population. However, all three sex ratios were not significantly different to a balanced ratio when tested against proportions expected under a 1:1 ratio (Yates $\chi 2$ tests, all $P>0.05$; Table 4.10). This may reflect no significant deviations from a 1:1 sex ratio, or reduced statistical power associated with such small samples. From these tests alone it is therefore difficult to ascertain if this ratio could be observed due to chance alone.

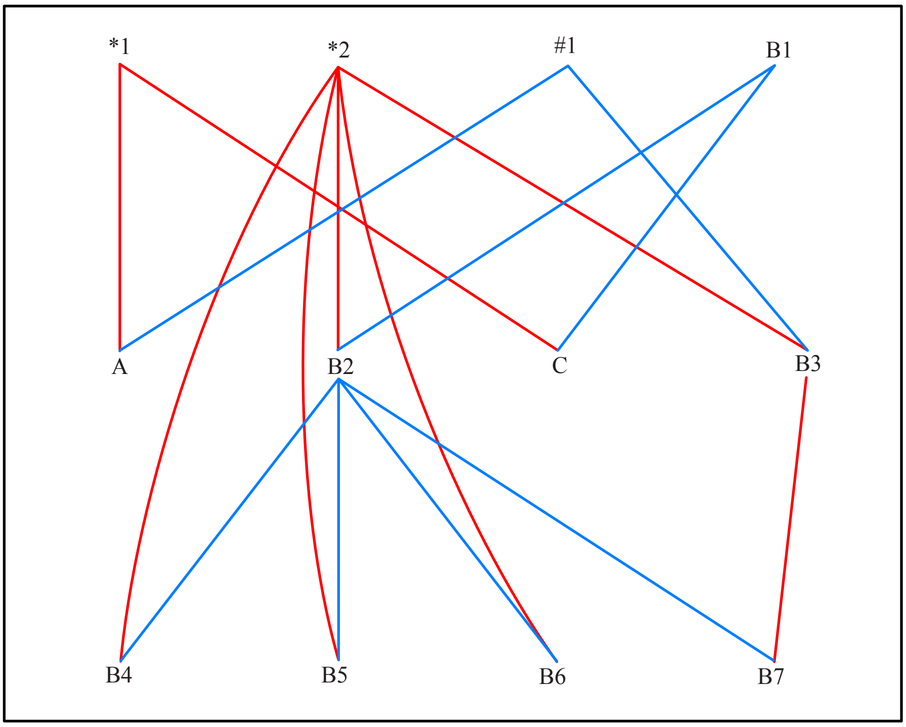


Figure 4.8 Pedigree constructed from ML configuration of relationships between individuals in the current population. Red lines correspond to paternal lines; blue lines correspond to maternal lines. Probable (theoretical) fathers and mothers not sampled in the study but inferred by COLONY based upon observed genotypes of sampled individuals are represented as starred (*) and hashed (#) numbers respectively.

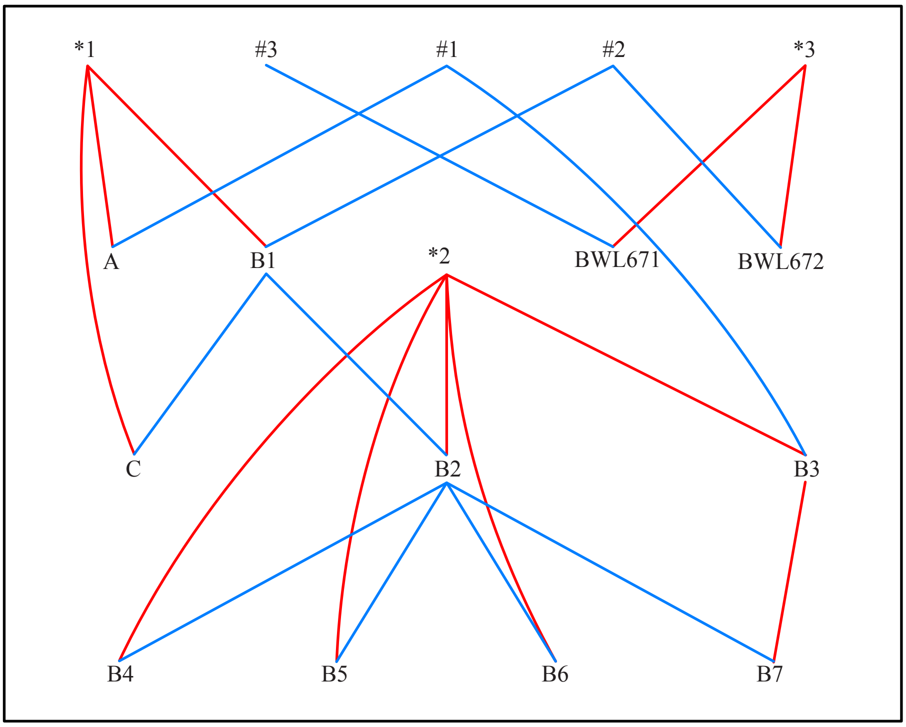


Figure 4.9 Pedigree constructed from ML configuration of relationships between individuals in the current population and most recently collected museum specimens (BWL 671 and BWL 672, c. 1980) -caption as per Figure 4.8.

Table 4.8 ML relatedness coefficients (*r*) indicating pairwise relatedness between all sampled individuals of current population, and between these individuals and the two most recent historical museum specimens (BWL 671 and BWL 672, c. 1980). Increasing values of *r* from cousins (0.125) to level of parent-offspring or full-siblings (0.5) indicated by increasing intensity of grey shading. Social groups outlined in bold boxes and historical specimens separated from current populations samples by dashed lines.

	A	B1	B2	B3	B4	B5	B6	B7	C	BWL671	BWL672
A	1										
B1	0.08	1									
B2	0.15	0.05	1								
B3	0.50	0	0.27	1							
B4	0	0.09	0.63	0.55	1						
B5	0.15	0.05	0.85	0.27	0.63	1					
B6	0	0.09	0.63	0.55	0.88	0.63	1				
B7	0.27	0.01	0.32	0.84	0.76	0.32	0.76	1			
C	0.38	0.59	0.25	0	0	0.25	0	0	1		
BWL671	0	0	0	0	0	0	0	0	0	1	
BWL672	0	0.17	0	0	0	0	0	0	0.13	0.35	1

Table 4.9 Results of sex-determination genotyping for the current population. ‘Observed sex’ corresponds to that inferred by long term observation; ‘Sex by genotype’ refers to that inferred by Amelogenin genotyping for faecal samples from individuals.

Current population individual	**Consensus genotype**	**Observed sex**	**Sex by genotype**
A	103-109	male	male
B1	103-103	female	female
B2	103-103	female	female
B3	103-109	male	male
B4	103-109	*unknown*	male
B5	103-103	*unknown*	female
B6	103-109	*unknown*	male
B7	103-109	*unknown*	male
C	103-109	male	male

Table 4.10 Sex ratios for the current population and results of tests for deviation from an even sex ratio (1:1 males to females) using Yates-corrected Pearson’s Chi-squared statistic (χ^2). Degrees of freedom for all tests=1, sample size used to calculate ratios indicated by *n*.

Sex ratio tested	**Females**	**Males**	**Observed ratio (female:male)**	**Yates-corrected Chi-square test (χ2) against 1:1**	
Current population sampled (*n*=9)	3	6	1 : 2	Yates χ2	0.44
				P	0.50
Group B (*n*=7)	3	4	3 : 4	Yates χ2	0
				P	1
Group B offspring only (*n*=4)	1	3	1 : 3	Yates χ2	0.25
				P	0.62

Discussion

The genetic state of the Hainan gibbon

Temporal decline in diversity

This study represents the first investigation of the genetic health of the sole remaining Hainan gibbon population within the context of the species' genetic history. The low genetic diversity detected for the current population across all metrics supports the findings of the only previous investigation of the species' genetic diversity. Li et al. (2010) quantified diversity in terms of nucleotide diversity 'π', which measures the average number of pairwise differences between any two sequences. This is not directly comparable to the measures of diversity derived here, but the species' nucleotide diversity was found to be exceptionally low, at $\pi=0.0083$. This is substantially lower than that reported for other gibbon species: Kim et al. (2011b) observed levels of π in *Nomascus* and *Hylobates* species, from 0.23-0.26% and 0.24-0.47%, respectively, and slightly lower levels for the *Symphalangus syndactylus;* (0.15%) and *Hoolock leuconedys* (0.19%). Together, this work, along with the findings presented here, indicates the remaining Hainan gibbon population is suffering from limited genetic diversity.

In this study I was able to demonstrate however, that this low genetic diversity does not represent a long-term pattern for the species, but is evidently the direct result of the recent past bottleneck experienced by the population. Despite generally low levels of polymorphism in both temporal samples, likely the result of the cross-amplification approach, significant reductions in heterozygosity and allelic diversity were apparent, indicating that the genetic diversity of the Hainan gibbon has declined since the beginning of the 20th century, and even within the last 30 years. The current population possesses approximately 69% of the heterozygosity, and 68% of the allelic richness of the historical population. This decline was detected even with limitations to the historical dataset (sample size and number of loci fully genotyped); therefore these estimates may actually be a conservative estimate of the amount of genetic diversity lost. Regardless, the decline in diversity detected corresponds closely to the difference in diversity reported for threatened species generally, which on average possess around 65% of the microsatellite diversity of related, non-threatened counterparts (Frankham et al. 2009). Furthermore, similar within-species temporal declines in diversity following severe bottlenecks have been documented in other threatened species: H_e reportedly declined by 52% and *Na* by 32% in the black-footed ferret (*Mustela nigripes*) (Wisely et al. 2002); and H_e fell by 57% and *Na* by 55% in the Mauritius kestrel (Groombridge et al. 2000). 'Ghost' alleles (Bouzat et al. 1998) present in the historical Hainan gibbon population were absent from the current population for a number of loci, indicating loss of allele forms over time as a result of the bottleneck. The overall pattern of temporal sample dispersion detected by PCoA, with historical samples distributed in a funnel-shaped spread narrowing down towards the more tightly clustered current population, also supports the detected decline in diversity, and the documented historical contraction in geographic range of the species across Hainan, to its present, highly restricted distribution (Liu et al. 1984, Zhou et al. 2005).

This decline has led to significant differentiation of the current population from the historical. The degree of differentiation detected (F_{ST}=0.15) is virtually identical to that observed for geographically-separated populations of Kloss's gibbon (*Hylobates klossii*) in the Mentawi Islands (F_{ST}=0.157, Whittaker 2009), although that differentiation was not statistically significant. As such, the differentiation observed between the remaining Hainan gibbon population and its recent historical state is equivalent or greater than separate island populations of *H. klossii* which have been isolated for around 7,000 years. This degree of differentiation is also in-line with that observed for persisting subpopulations of other threatened species: largely disconnected populations of the Critically Endangered Sumatran tiger (*Panthera tigris sumatrae*) show the same value (F_{ST}=0.15) (Smith 2012); and partially-disconnected populations of the Endangered Ethiopian wolf (*Canis simensis*), show values of this magnitude or greater (Gottelli et al. 2004). The differentiation between temporal samples is not as great, however, as that between species within the genus *Nomascus*, estimated at between $F_{ST=}$0.30-0.56 (Chan et al. 2013), which is similar to that observed between bonobos and chimpanzees (Fischer et al. 2006). The Bayesian population STRUCTURE analysis supports genetic distinction of the current population from the historical samples, even when the historical sample is split into two populations (intermediate: 1960s-1980s, and distant historical: 1899-1911), indicating further differentiation of the Hainan gibbon population in recent decades. The assignment of 3.5% of the current population to these two historical populations indicates that only a very small amount of historical genetic diversity persists in the current population within two individuals; B1 and the male from Group C. One of these individuals (B1) is already post-reproductive and reportedly up to 45 years old (Li et al. 2010). Thus, the diversity of the population will decline further following the death of this individual.

Evidence of multiple bottlenecks

Endemic island species may show diminished genetic diversity as a result of an evolutionary history of sustained isolation and small effective population size, a founder effect, or a more recent crash in population size (Frankham 1997, Groombridge et al. 2009). The evidence of a recent past bottleneck having produced the observed reduction in diversity in the current Hainan gibbon population is compelling. There has been a clear shift in the mode of allele frequencies from the historical to the current population, and the effective population size of the current population is exceptionally low. However, there is also evidence for a bottleneck in the historical sample, with significant heterozygosity excess and a small N_e (as estimated by the single-sample metrics) detected for both temporal samples. This could be attributed to the limitations of the approaches employed for the given sample sizes: all single-sample estimators of N_e suffer when sample size is small ($n < 20$ individuals) and/or the number of markers used to assess the population is restricted (England et al. 2006, Wang 2009). Indeed, the single-sample estimates of historical N_e (overall range 2.8-16) were much lower than we would expect for the historical period (1899-1980), given population estimates suggest at least 2,000 individuals remained in the 1950s (Liu et al. 1984), and 500 individuals in the 1970s (Zhou et al. 2005).

The Bayesian approach was more informative, revealing a clear temporal reduction in N_e between the time of the oldest sample and the current population, resulting in the extremely small current N_e (2.15). The observed ratio of the current N_e to the total current population size, N, (2.15:25= 0.086) is in-line with that found by Frankham (1995) for 102 species: mean ratio from comprehensive estimates in the order of 0.10. This result is particularly alarming as studies of wild populations indicate that an effective population size of less than 50 can significantly decrease population viability (Westemeier et al. 1998, Madsen et al. 1999) and an effective population size of at least 1,000 is required to maintain evolutionary potential in perpetuity (Frankham et al. 2014). The analysis does not allow us to determine the exact timing of the Hainan gibbon population crash, but it seems likely that the worst decline occurred after the collection date of the most recent historical samples (1980); an approximation supported by available population estimates for this period (Wang and Quan 1986, Liu et al. 1989, Liu and Tan 1990). This follows the worst phase of forest loss across Hainan, with primary forest cover reported to have shrunk from 35% in the early 1950s, to less than 10% in the 1980s (Li 2004). It also coincides with a period of limited financial support for the management of BNNR (early 1990s) associated with changing political administration on Hainan, which reportedly led to additional forest clearance and hunting of gibbons during that time (Zhang 1992, Zhang and Sheeran 1993).

The assessment of change in N_e over time also revealed that the population size at the time of the oldest sample, 1899, was already relatively small. The modal Bayesian estimate indicates an ancestral N_e of c. 1,000 which, following the expected N_e:N ratio (0.10), would suggest an overall population of around 10,000 gibbons at that time. The large HPD confidence limits associated with this estimate make it uncertain, but this indication of a modest Hainan-wide abundance even at the end of the 19th century is supported by historical accounts of the time. Swinhoe (1870) alluded to a general rarity of the species and reported great difficulty in observing a live (wild or captive) specimen during his expedition. There is also evidence of populations of other gibbon species being lost from mainland China during this period as a result of anthropogenic pressures, primarily forest loss and unsustainable hunting levels (van Gulik 1967, Wen 2009), and reports the Hainan gibbon population was subject to similar pressures at this time (Chan et al. 2005). Similarly, several other large mammal species reported to occur in Hainan in the late Ming and Qing Dynasties, including dhole (*Cuon alpinus*), serow (*Capricornis milneedwardsii*), and possibly Père David's deer (*Elaphurus davidianus*), appear to have disappeared by the start of the 20th century (Dobroruka 1970, Wen 2009). This would suggest that mammal populations on Hainan were already being impacted by human activities by this time. Thus, it appears that the Hainan gibbon population may have suffered an earlier decline, as well as the recent severe population crash in the 20th century. An earlier population decline would also explain the relatively low level of polymorphism seen in the historical sample and perhaps why tests of heterozygosity excess revealed significant evidence of a bottleneck in the historical population. Regardless, the obvious temporal change in N_e and significant drops in diversity metrics between historical and current populations, indicate that the population suffered a further decline in genetic diversity as a result of the precipitous population decline in the 20th century, producing the highly impoverished levels observed today. Furthermore, the magnitude of the current N_e indicates that despite some limited recent population recovery, from an estimated 13 individuals in 2003 (Chan et al. 2005) to the current estimate of c. 25, many additional generations of mutations will be required for the effective population size to recover to the historical levels indicated by this analysis. This work thus adds to a growing body of literature demonstrating the importance of contextualising measures of genetic condition for currently threatened populations against both the species' historical genetic status, and a chronology of past population dynamics and human impacts, to reveal the nuanced insights required for conservation management (Groombridge et al. 2009, Raisin et al. 2012, Bristol et al. 2013).

Inbreeding, relatedness and biased sex ratio

Direct evidence of inbreeding within the population was limited, with non-significant inbreeding coefficients derived for both temporal samples. However, individuals in the remaining population appear to be related at the level of half to full-siblings between social groups, and full-siblings or parent-offspring within a social group. Crosses at this level of relatedness will theoretically increase the inbreeding coefficient by 0.15 after as little as two generations, and 0.35 after four, reaching 1.0 (complete inbreeding) after around 20 generations (Hartl and Clark 1997). Thus, if all individuals in the population are indeed this closely related, inbreeding is only likely to increase in the population in the future. Li et al. (2010), using only six samples from one group, reported four haplotypes within Group B. My results indicate a higher level of relatedness, with only two maternal lines present in this group's pedigree. These results may be limited by the restricted population sample and/or low polymorphism for the few loci genotyped implying closer relationships than may actually exist (Kalinowski et al. 2006, Jones and Wang 2010). However, the pedigree was derived from more extensive sampling of the population (samples from three groups), and therefore is likely to more accurately represent relatedness than the previous assessment. Kenyon et al. (2011) detected full-sibling relationships between adults from neighbouring *Nomascus gabriellae* groups within Cat Tien National Park, Vietnam. Therefore, the level of relatedness detected between Hainan gibbon social groups seems realistic, but a general lack of comparable data from other gibbons makes it difficult to assess whether the level of relatedness within the Hainan gibbon population indicates closer than average relatedness. Furthermore, while direct comparisons are limited by differences in methodology and social and mating systems, studies of other previously bottlenecked populations of threatened taxa have revealed similarly elevated levels of relatedness within social clusters (e.g. northern hairy-nosed wombat (*Lasiorhinus krefftii*), Taylor et al. 1997; black-handed spider monkey (*Ateles geoffroyi*), Hagell et al. 2013).

The molecular sex determination indicated a male-biased ratio of offspring in Group B (3:1), concurring with that previously reported for the species based upon visual observations alone (Liu et al. 1989). Even with the Yates correction, the small samples limit the ratio tests, and as such it is impossible to determine if such a ratio might be observed by chance alone. Evidence exists however for male-skewed sex ratios at birth in a number of ex-situ gibbon populations which are similarly small. Jago and Melfi (2010) detected a male bias of 67-90% for three gibbon species kept in European zoos, despite captive management. These authors did not document the level of relatedness within the populations, but they did detect a significant statistical association between the degree of sex-bias and the gross energy provided within the captive diet administered. Females on lower calorie diets were more likely to produce male offspring, indicating that the ratio of offspring may be influenced by both genetic and environmental effects in gibbon populations. Given concerns regarding habitat condition within BNNR, these findings have important management implications for the Hainan gibbon population.

Potential limitations

This study possesses the limitations inherent in all conservation genetics studies of rare and threatened species; issues of sample size and potentially reduced statistical power. Theoretically, smaller samples may detect lower diversity simply through sampling bias, meaning the inferential power of diversity analyses and detection of any decline in diversity may be constrained by the small n and number of loci used to characterise the species' past and present genetic condition. However, n has been found to have very little effect on measures of H_e or pairwise F_{ST}, even when only five individuals are genotyped at as few as 10 loci (Smith 2012). I adopted unbiased estimators of H_e and F_{ST} which take n into account, meaning the estimates may have high sample variance but their magnitude should be relatively accurate. I also used rarefaction to assess Ar, which accommodates unequal population samples, and employed non-parametric significance tests for all comparisons, meaning that the significant differences detected are likely to be accurate. Furthermore, significant biological effects discovered under small n have been detected despite the reduced sample, meaning the effect must be considerable to have been detected. For example, the decline in diversity was distinguished despite a reduced historical sample (consensus genotypes at only seven loci for all eight historical samples, and for only seven samples across all 11 loci). Therefore, the differences detected are likely to be valid.

It could be argued that the detected decline in diversity may, however, be a factor of temporal and spatial sampling bias. The historical 'population' samples for which DNA extraction was successful spanned a period of 81 years; although four of these samples were collected from BNNR, the other four were from unrecorded localities on Hainan. By comparison, the current samples represent a snapshot of the population from one location. This was an unavoidable constraint of the limited samples available, and such drawbacks to temporal comparisons using museum specimens and samples from critically small, remnant populations are not unique to this study (Groombridge et al. 2000; 2009, Gottelli et al. 2004, Holbrook et al. 2012). Despite this constraint, Bayesian assessment of change in N_e, which takes into account the exact date of each sample, supported a bottleneck having occurred within the Hainan gibbon population. There was also clear evidence of genetic differentiation between current and historical samples, indicating that there has been a shift in the genetic composition of the species over time. Additionally, even in the absence of any historical context, the diversity remaining in the current population appears to be exceptionally low. This is unlikely to be the result of genotyping error, as conservative genotyping rules were employed to derive the consensus genotypes. Furthermore, the population also shows other hallmarks of a genetically-compromised population including a high level of relatedness and evidence for a biased sex ratio. Therefore, regardless of any potential sampling bias, the conclusions regarding the current genetic status of the remaining population stand. Nevertheless, further investigation employing Next Generation Sequencing techniques (e.g. using a whole-genome approach to discover Single Nucleotide Polymorphisms), which would permit assessment at a large number of genomic sites and so provide finer-resolution information, would be invaluable to validate these findings, and remains a promising next step.

Management implications

The reduced genetic diversity in combination with the extremely low N_e of the current population may have important implications for the long-term viability of the species, being likely to make the population more vulnerable to disease and sudden environmental changes.

Diminished genetic diversity could also have ramifications for the species' fate in the face of future climate change, with a recent study revealing that rapid environmental change can limit mutational opportunities, and certain genotypes that would be selected under milder conditions can become inaccessible under such situations (Lindsey et al. 2013). In an already genetically-compromised population, any such effect is only likely to be compounded. The outcome of diminished diversity is not certain, however. Critically Endangered species may persist despite reduced diversity. The Iberian lynx (*Lynx pardinus*) has maintained extremely low genetic diversity for at least 50,000 years (Rodríguez et al. 2011), and the koala (*Phascolarctos cinereus*) has been characterized by low mtDNA diversity for at least the last 120 years (Tsangaras et al. 2012). However, both of these species consist of more than one population, which means that they are, comparatively, less vulnerable to stochastic effects which could eliminate the last Hainan gibbon population.

Ideally, a strategy of 'genetic rescue' where genes are introduced from other populations (wild or captive) would be implemented to improve the genetic state of a threatened population with low genetic diversity (Hedrick and Fredrickson 2010). For example, endangered populations of the Florida panther (*Puma concolor coryi*) and the grey wolf (*Canis lupus*) have been successfully restored by genetic enhancement via inter-population translocation (Vilà et al. 2003, Johnson et al. 2010). Unfortunately, such an approach is not an option for the Hainan gibbon; the remnant population constitutes the last population, and there are no captive individuals within or outside China. Thankfully, it appears other species have managed to recover from critically low sizes, despite severe losses of genetic variability following an extreme bottleneck, without the addition of new genetic variation, e.g. Chatham Islands black robin (*Petroica traversi*) (Ardern and Lambert 1997), Mauritius kestrel (Groombridge et al. 2000), Mauritius parakeet (*Psittacula echo*) (Raisin et al. 2012). Such recoveries have only been achieved through intensive, carefully planned conservation management, indicating that reduced genetic diversity may not preclude conservation activities, but must be considered during conservation planning.

Long-term recovery of the Hainan gibbon is likely to require such intensive management, for example, translocation of a subset of the population to establish a new founder population (see Chapter 6), and the findings regarding the relatedness of individuals in the current population have important implications in this regard. As all remaining individuals appear to be related at the level of half to full siblings, it will be crucial to take these associations into account for the continued viability of both the source population and that of any founder populations under such an action. However, for a gregarious, group-living species with complex social behaviours, selection of individuals for translocation based upon attempts to maintain genetic integrity must be coupled with consideration of maintenance of social integrity, which may lead to more nuanced recommendations. The close relationships and evidence of inbreeding also suggest it may be necessary to adjust overall expectations of likely rates of population recovery, as lowered reproductive fitness and reduced survival have been observed in other populations of endangered species suffering inbreeding (Madsen et al. 1996, Swinnerton et al. 2004, Hemmings et al. 2012). Attention should focus on preservation of all remaining individuals to prevent any further decline in diversity and losses to the breeding pool. Consequently, eliminating the threat of hunting absolutely is paramount, as is the reduction of other anthropogenic actions that are currently degrading the BNNR habitat. Increasing available habitat may also support population growth, reduce environmental impacts to the sex-ratio of offspring, and allow the population to withstand localised environmental threats in the face of its reduced diversity.

Chapter 5. Comparative analysis of intrinsic versus extrinsic correlates of Hainan gibbon ranging behaviour and social organisation

Introduction

The decline and endangerment of species is typically not due to a single cause, but is instead the result of a complex combination of interacting factors (Crandall 2009). Consequently, for conservation efforts to have the best chance of succeeding, they must identify and address the drivers of a species' decline, and consider the behavioural, ecological, and demographic parameters which will influence its ability to persist in small numbers and ultimately recover (Caughley 1994). To date, conservation efforts for the Hainan gibbon have predominantly focused on mitigating the external factors that have been identified as responsible for the population's decline, namely habitat clearance and targeted hunting, in addition to population monitoring (Chan et al. 2005, Zhou et al. 2005, Lin et al. 2006a). More intensive, active management of the surviving population has been largely constrained by a deficit of robust data and general lack of clarity regarding even the species' basic ecology. Crucially, it remains unclear which aspects of the observed ecological and behavioural characteristics of the tiny remnant Hainan gibbon population may be "natural" for the species even before human impact, and which may be artefacts of the population's presently compromised situation. This lack of data represents a major barrier to effective conservation planning, as it is difficult to assess which factors might be managed and which aspects of the species' biology are unlikely to change despite intensive management.

Gibbons are generally considered to be monogamous, territorial apes, showing relatively consistent patterns of diet, territory and home range size, group composition and mating strategy, despite occurring in several different forest environments (Chivers et al. 2013). Gibbons typically occur in small monogamous social groups, consisting of a nuclear family containing an adult male, an adult female and one to three offspring, which maintain relatively small home ranges of about 0.40 km^2 (Bartlett 2007, Chivers et al. 2013). The Hainan gibbon appears to be remarkable in terms of these key general behavioural, ecological and demographic characteristics, with multiple reports of large (>6 individuals on average, with observations of up to 12 individuals in one group), polygynous groups maintaining much larger home ranges (estimates between 1.5-10 km^2) (Liu et al. 1987, 1989, Liu and Tan 1990, Wu et al. 2004, Chan et al. 2005, Zhou et al. 2008a, Zhou et al. 2008b, Li et al. 2010, this study: Chapter 3). The drivers behind these apparently anomalous ranging and social habits are not clear. It has been suggested that these features may constitute either typical characteristics of Hainan gibbon biology (Liu et al. 1989, Wu et al. 2004) or, alternately the population's response to extrinsic pressures, with reduced habitat availability and suboptimal habitat quality in BNNR potentially driving large home range requirements, which in turn may prevent the establishment of new social groups and force individuals to remain within their natal groups (Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b). Alternatively, or additionally, limited mating opportunities generated by the greatly restricted population size may explain the observed polygynous mating system as an abnormal behaviour (Bleisch and Chen 1991, Chan et al. 2005), and a lack of neighbouring groups could be permitting the expansion of the existing group home ranges (Fellowes et al. 2008).

To inform conservation efforts for the Hainan gibbon, it is vital to understand the intrinsic versus extrinsic drivers of these behaviours, which requires wider consideration of ecological and behavioural patterns observed under different environmental conditions across other gibbon species. The conventional description of gibbon ranging and social organisation is largely rooted in observations of *Hylobates* gibbons, dating back to the seminal work of Carpenter (1940). However, as additional wild populations of an increasing number of species have been studied, it has become apparent that while these general habits may still be predominant, gibbons show much greater variation than suggested by the typical description of gibbon ecology and behaviour given above. Across the Hylobatidae, occurrences of single social groups containing more than two adults make up 10% or more of all groups studied (Fuentes 2000), and within-family variability in group size and ranging behaviour has also been reported (Malone and Fuentes 2009). *Nomascus* gibbons in particular seem to show considerable variation, with observations of large group sizes (average >6 individuals) and home ranges (1.3-1.5 km^2), and polygynous groups in *N. nasutus* (Geissmann et al. 2002, Chan et al. 2008, Fan et al. 2010, Fei et al. 2012) and *N. concolor* (Haimoff et al. 1986, 1987, Sheeran 1993, Jiang et al. 1999, Fan et al. 2006, Fan and Jiang 2008a, b, 2010). Like the Hainan gibbon, these other *Nomascus* species are Critically Endangered (Bleisch and Geissmann 2008, Bleisch et al. 2008b), with greatly restricted population sizes and limited available habitat which is isolated and disturbed (Fan et al. 2006, Mootnick et al. 2012). Consequently, these observations could support a disturbance hypothesis, with anthropogenic pressure and habitat alteration driving observed patterns, and indicating ecological flexibility in gibbon behaviour (Malone and Fuentes 2009). Alternatively, the apparent occurrence of these features in the sister species *N. hainanus* and *N. nasutus* and the closely related *N. concolor* (see Thinh et al. 2010a) may point to these traits being evolutionarily characteristic for crested gibbons, or at least these basal representatives of *Nomascus*. This would instead indicate intrinsic, phylogenetically-driven patterns of ecological and behavioural variation within the Hylobatidae.

Despite the importance of clarifying the drivers of these Hainan gibbon ecological and behavioural parameters to best-practice conservation planning for the species, beyond simple descriptive comparisons to other crested and non-crested gibbons (e.g. Chan et al. 2005) there has been no formal attempt to contextualise the species' home range and social organisation within the patterns seen across the Hylobatidae. The comparative approach, whereby statistical methods are used to test for correlations between variables, taking into account phylogenetic non-independence between species (Fisher and Owens 2004), has been widely employed to inform broad-scale conservation efforts. For example, macroecological landscape-level and higher taxonomic-level (phylum, class, order) comparative analyses have been used to identify underlying predictors of extinction risk (Purvis et al. 2000, Cardillo et al. 2005, Cardillo et al. 2008) and assess determinants of mammalian population declines (Fisher et al. 2003, Collen et al. 2011). This approach has also been employed to provide a basis for prioritising conservation actions; for example, through assessment of which species are more likely to benefit from intensive intervention actions such as captive breeding (Clubb and Mason 2003) and translocation (Wolf et al. 1998). Comparative analyses assessing correlates of patterns within lower-level taxa (e.g. families) are less common (but see Freed 1999). However, this approach may be focused to identify intrinsic and extrinsic drivers of variation in ecological and behavioural traits seen within individual groups of interest (e.g. Ossi and Jason 2006, Lehman 2007), thus representing a valuable tool to inform conservation management of individual species.

This study aimed to provide new insights for Hainan gibbon conservation by employing a comparative approach to assess the potential drivers of home range size, social group size, and mating system across the Hylobatidae. To determine the contribution of intrinsic versus extrinsic factors to variation observed for these key traits between different gibbon species, I first assessed the evidence for a non-random distribution in trait variation within the context of phylogenetic relationships or 'phylogenetic signal' in each trait. I then used predictive models within a phylogenetic framework to examine which of a range of intrinsic and extrinsic factors may explain or predict within- and between-species variation seen across the Hylobatidae. Putative predictors include those biological and abiotic factors hypothesised to be associated with these traits. Tests of observed versus expected values under full (Brownian) phylogenetic signal and assessment of regression patterns were then used to investigate whether the Hainan gibbon is markedly different in key traits when compared to other gibbon species. These analyses represent the first attempt to systematically assess the evidence for phylogenetic versus non-phylogenetic control of key behavioural, ecological, and demographic traits across the Hylobatidae. The results provide insights directly relevant to the conservation management of the Hainan gibbon, as well as wider implications for understanding general gibbon ecology.

Methods

Data collection

Comparative dataset

A comparative dataset was compiled containing data on the three response variables of interest: home range (HR), group size (GS) and mating system (MS). Data were collected from available resources for the 19 currently recognised gibbon species (after Chivers et al. 2013), including published and grey literature. HR and GS values employed for the Hainan gibbon were those derived within this study (see Chapter 3), as the most recent available data for the species. I aimed to include observations for as many gibbon populations (separate study sites) as possible in order to capture intraspecific as well as interspecific variation, to permit detection of extrinsic, site-level influence as well as phylogenetic influence upon the expression of response traits. As site-specific quantitative data for the variables of interest were not always explicitly contained within the available literature, I supplemented the comparative dataset by directly surveying gibbon researchers who have knowledge and present or past experience at as many gibbon study sites as possible (see Appendix G for standardised questions included in questionnaire). This combined approach captured comparative data for 39 populations across the 19 species (Appendix H). Data from more than one population (different sites) were obtained for 58% of gibbon species, with further data collection limited in some cases by the existence of only a single extant or studied population per species.

Predictor variables

In addition to the three response variables of interest (HR, GS, MS), site-specific data for eleven potential predictors were collected for use in predictive modelling analyses (Table 5.1). To avoid over-parameterisation, only data on key intrinsic and extrinsic variables which were hypothesised *a priori* to influence these response traits were incorporated, as recommended for predictive modelling in evolution and ecology (Burnham and Anderson 2002, Grueber et al. 2011).

As social frugivores, members of gibbon social groups range and feed together, and fruit (particularly fig) availability and load at sites may be an important predictor of HR size in gibbons (Chivers et al. 2013). Group size and density have been found to increase in locations with higher fruit tree densities (Mather 1992, Marshall and Leighton 2006, Chivers 2013). As site-specific information on gibbon food tree densities was predominantly unavailable, I used data on underlying site conditions that are likely to determine food tree density at a site. The following fundamental extrinsic variables were included, which capture site climatic conditions, potential productivity, and also possible thermoregulatory constraints to behavioural traits (e.g. activity budgets, daily path lengths): **latitude, longitude, altitude, annual mean temperature,**

Table 5.1 Potential intrinsic and extrinsic predictor variables (fixed effects) hypothesised to influence response traits and tested in predictive models, with data scale and source(s).

Potential predictor variable	**Scale**	**Source(s)**
adult body weight (kg)	species mean	Smith and Jungers (1997), Isler et al. (2008), Rowe and Myers (2011), WAZA (2012), Chivers et al. (2013)
group density (mean number of groups/km^2)	mean at site	As per Appendix H
latitude (decimal degrees)	exact value for site	As per Appendix H
longitude (decimal degrees)	exact value for site	As per Appendix H
altitude (metres a. s. l.)	mean for site across years, 1km resolution	WorldClim Global Climate Dataset V.1: Hijmans et al. (2005)
annual mean temperature (°C)	mean for site across years, 1km resolution	
annual precipitation (mm)	mean for site across years, 1km resolution	
precipitation seasonality (coefficient of variation)	mean for site across years, 1km resolution	
normalized difference vegetation index (NDVI; ratio)	mean for site across years, 8km resolution	Global Inventory Modelling and Mapping Studies Dataset: Tucker et al. (2005)
Global Human Footprint (GHF; %)	mean for site across years, 1km resolution	Global Human Footprint dataset V.2 (1995−2004): WCS and CIESIN (2005)
reserve area (km^2)	value for reserve	As per Appendix H

and **annual precipitation**. Latitudes and longitudes were collated from the literature and site location coordinates were reported by respondents to the survey. Mean altitudinal and climatic data were extracted from the WorldClim Global Climate Dataset V.1 (Hijmans et al. 2005) using a spatial query approach within ArcMap V.10.0 (ESRI 1999-2010) whereby the site location was used to derive standardised mean values for each site.

An additional, more direct measure of productivity, the **normalized difference vegetation index** (NDVI), was also included as a surrogate for vegetation structure and therefore annual productivity and biomass. NDVI correlates strongly with vegetation and general above-ground net primary productivity (Gong and Shi 2003, Pettorelli et al. 2005). I calculated average annual NDVI scores for each site, again using a map-based approach to extract values from the Global Inventory Modelling and Mapping Studies (GIMMS) Dataset (Tucker et al. 2005), which consists of 16-day composites spanning 1982-2011. Averaging the values across years also controls for atmospheric artefacts associated with satellite images (e.g. cloud cover; Nilsen et al. 2005).

Bartlett (2009) argued that ecological constraints play a key role in limiting gibbon HR, GS and MS, with seasonal variation in daily path length driven by seasonal variation in resources setting the home range and so number of females defendable. Chivers et al. (2013) explained general patterns of gibbon territoriality and monogamy through the apparently relatively small area that can be effectively defended in tropical forests, which will only support a small group size. The authors accounted for observed variation in home range and group size by suggesting larger areas are required to obtain sufficient resources in more seasonal environments, relaxing constraints to group size. Therefore, to capture inter-site variation in seasonality and thus any influence of this variable upon the response traits, I included **seasonality in precipitation** at each site. Precipitation seasonality data were obtained from the WorldClim Global Climate Dataset V.1 (Hijmans et al. 2005), with site-specific values derived using the spatial query approach as outlined above. Precipitation seasonality is calculated as the standard deviation of monthly precipitation estimates expressed as a percentage of the mean of those estimates; higher values represent more variable monthly rainfall and thus seasonality (Hijmans et al. 2005). NDVI also correlates with seasonal average energy availability (e.g. Nilsen et al. 2005, Wiegand et al. 2008), and therefore should have further captured this variable.

Low group density has been proposed as a possible explanation for the ostensibly larger HR and GS in the Hainan gibbon, as a result of greater available space for the extremely small population (Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b). Conversely, Brockelman et al. (1998) argued for delayed dispersal from groups, and thus potentially larger GS, in habitats saturated with gibbon groups. Therefore, to address the theory of limited space impacting HR, GS and MS, **gibbon group density** (number of social groups per km^2) at each site was determined and included as a measure of potential (intraspecific) site-specific competition for space and resources. The **area of the reserve** (km^2) in which the population is found was also included as a predictor, representing the available space at the site in lieu of specific data on amount of available (and gibbon-suitable) habitat, which was generally unavailable for most sites. Group density and reserve area data were collected from the literature, supplemented by survey responses from gibbon researchers.

Site condition, including habitat quality and extent, as well as habitat disturbance due to direct human impact (e.g. development, logging etc.), has been argued to be a potential driver of the purportedly anomalous HR, GS or MS observed for some gibbon populations (Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b, Malone and Fuentes 2009). To incorporate such external influences I also included a metric of anthropogenic disturbance, deriving site-level values from the **Global Human Footprint** (GHF) dataset V.2 (1995-2004) (WCS and CIESIN 2005). The GHF index expresses relative human influence as a percentage (ranging from 1-100), computed from spatial data incorporating human population density, land use, and infrastructure (including roads, railroads etc.); higher scores indicate greater human influence or impact in the area. This metric does not take into account smaller-scale threats (e.g. non-timber forest product harvesting, hunting), which are particular issues for gibbons but for which it is particularly difficult to obtain quantitative data. As such, the GHF was meant as a standardised proxy of human impact.

Finally, species mean **adult body weight** was included as a key intrinsic predictive variable and proxy for various life history traits which may interact with and influence a range of ecological and behavioural characteristics in primates and other mammals (e.g. reproductive rate, gestation period, weaning length, interbirth interval; Purvis et al. 2000, Cardillo et al. 2005). As no site-level body weight data were available, species-level data were employed, with the species mean replicated across all populations of that species. Where mean body weights were not available, medians were calculated from the range of body weights reported for a species by an individual literature source.

Phylogenetic tree

To incorporate phylogenetic relatedness between gibbon species into the analyses, I manually reconstructed a phylogenetic tree for the Hylobatidae within TreeEdit V.1.0a10 (Rambaut and Charleston 2002) based upon the most comprehensive inferred phylogeny available (Thinh et al. 2010a) with some essential amendments. Only full species were included. *Hylobates abbotti* and *H. funereus* were included as separate species, following their recent designation as distinct species rather than subspecies of *H. muelleri* (Chivers et al. 2013). The most recently described gibbon species, *N. annamensis* (Thinh et al. 2010b), was also incorporated based upon unpublished genetic divergence data which indicate this species split from *N. gabriellae* c.0.7 million years ago (Christian Roos pers. comm., September 2013). In the version of the tree used to test for phylogenetic signal, the lineage containing the two orang-utan species, *Pongo abelii* and *P. pygmaeus*, was included as an outgroup as the next oldest split in the Hominoidea. This subfamily was an appropriate outgroup, as orang-utans occupy similar and sometimes sympatric habitats to gibbons in south-east Asia, and exhibit biological differences to gibbons but also biological similarities, including suspensory locomotory behaviours and similar frugivorous diets supplemented with leaves, barks, flowers, and invertebrates (Williamson et al. 2013). Comparative data on the response variables were also collected from published sources (Singleton and van Schaik 2001, Isler et al. 2008, Singleton et al. 2008, Rowe and Myers 2011, Williamson et al. 2013) for these two species. The final phylogeny used in the analyses is shown in Figure 5.1. The Ponginae outgroup was not incorporated into the predictive model analyses. No polytomies were detected in the final tree, so any influence of poor tree resolution in the analyses can be discounted.

Data analysis

Continuous variables (predictor and response) that varied by an order of magnitude were log-transformed prior to analysis to normalise distributions and equalize error variance. Additionally, GHF values, which are expressed as a percentage, were reduced to proportions and Arcsine transformed. Absolute values of latitude were employed. The categorical response variable, MS, was binary coded (polygyny = 1; monogamy = 0; for *Pongo* spp., solitary = 0). Data transformations and all analyses were carried out in R V.3.0.1 (R-Core-Team 2013).

Phylogenetic signal

Phylogenetic signal can be defined as the tendency for related species to resemble each other more than they resemble species drawn at random from a phylogenetic tree (Blomberg et al. 2003). To test for a phylogenetic signal in the continuous traits of interest, HR and GS, I employed species average values (across-population observations) and estimated Pagel's lambda, λ (Pagel 1999), via phylogenetic generalised linear models (PGLMs; Freckleton et al. 2002; revised version of code PGLM V.3.4 provided by R. Freckleton, October 2013) . Lambda is a quantitative measure of phylogenetic dependence, that gradually eliminates phylogenetic structure by multiplying off-diagonal elements of the variance-covariance matrix describing tree topology (i.e. covariances between pairs of species) by values between 0-1 (λ=0 corresponds to the complete absence of phylogenetic structure; λ=1.0 corresponds to complete phylogenetic dependence) (Pagel 1999). Values of λ=0 indicate trait evolution that is independent of

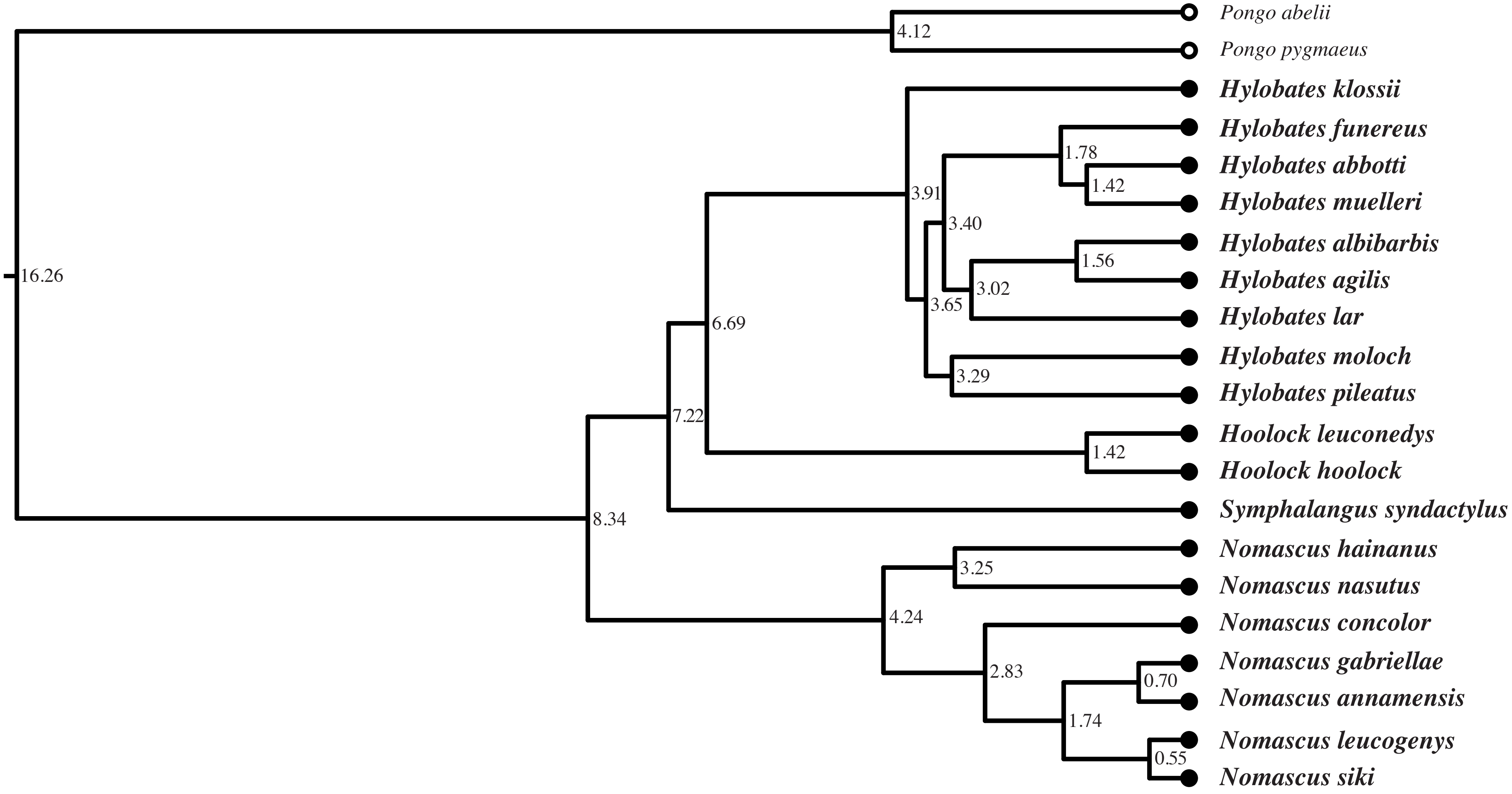


Figure 5.1 Phylogenetic tree of the Hylobatidae plus *Pongo* outgroup (indicated by hollow circles) used tests of phylogenetic signal and comparative analyses, with mean divergence times (million years ago) indicated at nodes; after Thinh et al. (2010a), Christian Roos (pers. comm., September 2013).

phylogeny and thus, on average, closely related species are not more similar than distantly related species; values of $\lambda=1$ indicate that the trait has evolved according to the Brownian motion model of evolution and closely related species tend to be more similar to one another than expected by chance (Freckleton et al. 2002, Kamilar and Cooper 2013). A PGLM estimates λ under maximum likelihood (ML) as well as log likelihoods at $\lambda=0$ and $\lambda=1$ to test if the observed ML model of λ is significantly different to models of no signal (0) or complete dependence (1) using likelihood ratio tests. As a control, I also tested for a polygenetic signal in body weight, as this trait has been shown to have significant phylogenetic signal in a wide range of bird and mammal groups (Freckleton et al. 2002), including primates (Kamilar and Cooper 2013), and therefore could be expected to also show a significant signal in gibbons.

Binary categorical variables cannot be tested using λ, so for the binary trait MS, I tested for phylogenetic signal using *D*, a measure for phylogenetic signal strength in a binary trait (Fritz and Purvis 2010), implemented within the "caper" package (Orme et al. 2013). *D* corresponds to the sum of changes in estimated nodal values of a binary trait along edges in a phylogeny. If a trait is phylogenetically conserved, the change in the trait value will only be between two basal clades, giving a sum of one (two differences between the root nodal value of 0.5 and the ancestors of the 1 and 0 clades). However, if the trait is labile, more changes will be observed between clades along the phylogeny, producing a higher summed value. Thus, values of *D* smaller than zero indicate highly conserved traits, and values greater than one indicate randomly dispersed traits (no signal). Again, the implemented test estimates *D* and the probability of observing the estimated *D* resulting from no phylogenetic structure, and from Brownian phylogenetic structure, by simulating *D* under each model and comparing the observed value to these model values. To assess *D*, I employed the predominantly observed MS for each species, which proved to be concordant (100% of cases) across the populations surveyed for each species. Comparative data for Ponginae were incorporated in all tests of phylogenetic signal.

Predictive models

Prior to running predictive models, correlations between the 11 predictor variables were assessed to check for collinearity amongst predictors. Correlation between predictors can confound conclusions about variable effects (making independent effects of each predictor hard to disentangle) and can be a particular problem for model selection under an information theoretic (IT) approach, as models with different predictors may have similar fits to data (Freckleton 2011). Correlation matrices and simple linear models were generated for each pairwise combination of predictors, but all pairwise comparisons yielded absolute correlation values and variance explained by linear models (adjusted R^2) of <0.5, indicating no issues of collinearity. Therefore all predictors were maintained.

Predictive regression models were constructed using the linear mixed-effects kinship model fit by maximum likelihood (lmekin) within the "coxme" package (Therneau 2012), a form of the linear mixed model that accounts for phylogenetic relatedness (non-independence) of observations from related species where more than one observation per species is incorporated. The lmekin model allows the phylogenetic relationships of multiple observations from related species to be incorporated as random effects via specification of two variance-covariance (VCV) matrices: one derived from the phylogenetic tree; and the other describing the within-species (here inter-population) variation to account for more than one observation per species and thus incorporate site-level effects. Covariance values decrease with increasing evolutionary distance between species, eventually reaching zero covariance for species that are sufficiently distant that they can be considered independent. When (population) samples come from the same species, covariance is specified as one, and as zero when samples are from different species. This method therefore uses population-level data and is thus able to consider the contribution of within-species variation while controlling for phylogenetic relationships of samples through an additional error component, i.e. a random variable for population level as well as species level. Accounting for the non-independence of samples thus allows fixed predictive effects to be understood.

Following a common approach in wide-scale comparative analyses (e.g. Harcourt 1998, Purvis et al. 2000, Collen et al. 2011), initially I conducted single predictor lmekin regressions of the three response variables (HR, GS, MS) against each predictor variable to examine the significance of each predictor separately. As a population's HR, GS and MS may be interlinked and one (or two) of these traits may determine the other, the response variables not being tested within a given predictive model were also used as predictors for each response in turn. Thus, in total 13 single predictor models were run per response. Predictors that were significant ($P<0.05$) were then incorporated into a global model for each response variable. This approach aimed to reduce the number of predictors within each global model to avoid issues of overparameterisation or overfitting of data and bias in regression coefficients, which occur when the sample size rule of thumb of 10:1 observations to predictors is violated in multiple regression (Harrell et al. 1985, Peduzzi et al. 1995, Peduzzi et al. 1996). A more recent study revealed that ratios of 5-9:1 perform similarly to 10:1 for Cox models (Vittinghoff and McCulloch 2007); therefore, a rule of at least >5 observations to one predictor was adopted. For $n=39$ populations this meant between 4-7 predictors, which was upheld by the number of significant predictors taken from each single regression for the global models. However, this precluded the incorporation of any predictor interaction terms, meaning that only main effects were fitted. Regardless, given the small sample size (which prevented more advanced analyses) and the absence of any correlations/collinearity in the predictors, this approach is likely to be sound.

The global model was not used as the final model, as a full model will contain estimates of all parameters -both significant and non-significant- which creates excess noise and reduced precision because each time a parameter is estimated, the information left is reduced (Whittingham et al. 2006, Burnham et al. 2011). As is appropriate when a range of potential explanatory variables that may be associated with a trait or behaviour are explored (Symonds and Moussalli 2011) using observational data from complex ecological systems (Johnson and Omland 2004, Whittingham et al. 2006), I employed an IT multimodel inference approach to model selection (Burnham and Anderson 2002, Burnham et al. 2011). Using the global model for each response, a set of candidate models were generated representing all unique combinations of the predictors in the global model. The candidate models (which included the global model and each single predictor model) were ranked using the Akaike Information Criterion (AIC) for model selection, which compares model fit and penalises models for greater complexity (Akaike 1973). For each model, the relative log-likelihood, AICc (second-order unbiased AIC corrected for small sample size; Hurvich and Tsai 1989) and ΔAICc (difference between each model AICc and best model AICc) were calculated, along with Akaike weights, w_i (measure of probability that model *i* is the best approximating model), using the "MuMIn" package (Bartoń 2013). To check the validity of the top-ranking (best approximating) model in each case, I used a model-averaging approach whereby a subset of models were used to produce parameter estimates and associated standard errors which are derived from weighted averages of these values across multiple models (Burnham and Anderson 2002, Symonds and Moussalli 2011). Models included in the subset were restricted to those with $\Delta AICc < 7$ (Burnham et al. 2011) which also corresponded to a cumulative $w_i > 0.95$ in all cases, thereby constituting a 95% confidence set (i.e. set which has 95% probability of including the best approximating model) (Burnham and Anderson 2002). The relative importance (RI) of each parameter after model averaging was calculated by summing the w_i across all models in which the parameter was present, producing an estimate of the probability that the given variable features in the best model.

Results

Phylogenetic signal

All three traits of interest (HR, GS and MS) were found to have significant phylogenetic signal. A strong phylogenetic signal was also detected for the control variable, body weight, indicating that this analytical approach was appropriate and the results for all traits tested are valid. Values of λ for HR, GS and body weight were all close to one under ML (Table 5.2). Furthermore, each ML-λ value for these traits was significantly different to zero but not significantly different from one, meaning that the λ value of each trait was not discernable from the Brownian expectation in every case. Therefore, these strong, significant patterns of phylogenetic signal suggest that more closely related species within the Hylobatidae resemble each other more in terms of their body mass, HR and GS than expected by chance. This indicates a phylogenetic association within the family-wide patterns of these traits and that to understand any other underlying (intrinsic or extrinsic) drivers of these traits, it was appropriate to control for phylogenetic relationships between the samples within the comparative dataset (as per the lmekin predictive models).

To ascertain if any gibbon species, particularly the Hainan gibbon, displays a HR or GS (or body weight as a control) exceptionally different to that expected under the observed, significant phylogenetic signal (ML-$\lambda \sim 1$), the PGLM derived for each trait was used to determine the value of the trait expected for each species based upon the values observed for all other species, and this value was compared to the observed value for that species (via Student's t-tests). The resultant *P*-values of these tests (after Bonferroni correction, adjusted *P*-value=0.0024) revealed no unusual body weight or GS values for any species (gibbon or orang-utan), with all observed values not significantly different to those expected according to the phylogenetic signal within each trait, despite the larger group sizes reported for some *Nomascus* species, including the Hainan gibbon (Table 5.3). However, for HR, three gibbon species (*N. concolor*, *N. hainanus*, *N. nasutus*) were detected as having observed home ranges that are larger, relative to all other gibbon species, than expected under the strong phylogenetic signal observed for this trait ($P<0.002$). Significantly extreme values were also detected for both *Pongo* species, but as these species exhibit exceptionally large ranges (mean HR *Pongo abelli* and *P. pygmaeus* are 19 km^2 and 16.75 km^2, respectively), and the prediction was focused on the Hylobatidae, this is not surprising.

A strong phylogenetic signal was also apparent in MS, with an estimated D= -1.386 indicating substantial phylogenetic clumping in the binary representation of this trait, and therefore that MS is highly phylogenetically conserved within the Hylobatidae. The associated probability of observing this value of D was not significantly different to that simulated under Brownian phylogenetic structure (P=0.945), but was significantly different to that estimated under no phylogenetic structure ($P<0.01$), indicating that the observed phylogenetic signal is significant. Given the manner in which D is calculated (i.e. as a contrast rather than a linear model), it was not possible to predict expected species manifestations of MS under phylogenetic signal in this trait nor, therefore, to conduct the same tests comparing the observed versus expected values for individual species as used for the continuous traits assessed under λ. As such, it was not possible to ascertain if the observed MS for any gibbon species is different to what might be expected under the observed phylogenetic signal, only that there was a significant signal for this trait.

Table 5.2 Tests of phylogenetic signal in two continuous traits of interest (home range and group size) and one control variable (body weight) using Pagel's λ under maximum likelihood (ML-λ) and tests against models of no signal (0) or complete phylogenetic dependence (1).

Variable	**ML-λ**	**Test**	χ^2	***P*-value**
body weight	0.9999	λ=0	45.38	1.62E-11
		λ=1	-0.01	1.0
home range	0.9999	λ=0	30.32	3.67E-08
		λ=1	-0.004	1.0
group size	0.9731	λ=0	20.61	5.62E-06
		λ=1	0.58	0.45

Table 5.3 Students t-test *P*-values for comparisons of observed trait values versus expected trait values under detected phylogenetic signal (ML-λ) for each gibbon and orang-utan (outgroup) species for two response traits and one control variable.. Significant values in **bold** (Bonferroni corrected *P*-value =0.0024).

Species	**Variable**		
	body weight	home range	group size
Hoolock hoolock	0.313	0.463	0.232
Hoolock leuconedys	0.420	0.344	0.160
Hylobates abbotti	0.406	NA	0.151
Hylobates agilis	0.474	0.118	0.216
Hylobates albibarbis	0.434	0.281	0.484
Hylobates funereus	0.295	0.490	0.474
Hylobates klossii	0.436	0.413	0.494
Hylobates lar	0.337	0.400	0.370
Hylobates moloch	0.413	0.491	0.216
Hylobates muelleri	0.437	0.488	0.377
Hylobates pileatus	0.364	0.461	0.311
Nomascus annamensis	0.321	0.214	0.110
Nomascus concolor	0.440	**0.001**	0.215
Nomascus gabriellae	0.395	0.110	0.088
Nomascus hainanus	0.461	**0.001**	0.110
Nomascus leucogenys	0.449	0.404	0.221
Nomascus nasutus	0.396	**0.002**	0.116
Nomascus siki	0.419	0.456	0.024
Symphalangus syndactylus	0.142	0.073	0.432
Pongo abelli	0.088	**<0.0001**	0.424
Pongo pygmaeus	0.184	**<0.0001**	0.126

Predictive models

Five predictors, as derived from significant terms detected in the single lmekin regression models, were incorporated into each global model for HR and GS, although not all terms remained significant when incorporated into the multiple regression models (Appendix I). This significance/non-significance of predictor terms depending upon the context of other parameters indicates an IT model selection approach was appropriate to reduce noise and improve model precision, as well as the ratio of observations to predictors. From the HR and GS global models, a set of 31 candidate models (including the global model and each single predictor model) were generated and ranked in terms of AICc. For HR, in addition to the best approximating model with lowest AICc, a total of 19 models with ΔAICc<7 were identified, which corresponded to a cumulative $w_i = 0.985$ and therefore the 98.5% confidence set (Appendix J). For GS, as well as the top-ranking model, 10 models with ΔAICc<7 were identified, which corresponded to a cumulative $w_i = 0.957$ and thus the 95.7% confidence set (Appendix K).

In the best approximating (final) HR model, when the covariance between population samples (expected under Brownian evolution) due to phylogenetic relatedness was taken into account, home range was explained by a population's group size, mating system, and gibbon group density at the site; larger home ranges were predicted by larger group sizes, the presence of a polygynous mating system, and lower group densities (Table 5.4). The total variance explained by the random (relatedness) effects was 0.00024, with 99.6% of this variance due to phylogenetic effects, and 0.43% contributed by inter-population variation within a species. The model-averaged coefficient estimates derived from the 98.5% confidence set of models agreed with the best-approximating model, with the same three variables detected as significant predictors and each having RI values of 0.70-0.84 (Table 5.5), indicating that the top-ranking model was valid and this model was the most parsimonious, despite 19 other models having some support (ΔAICc<7).

After taking into account sample non-independence due to phylogenetic relationships, the top-ranking GS model indicated larger group sizes were explained by mating system, specifically whether the population shows a polygynous mating system, and by lower annual precipitation at the site (Table 5.6). Annual mean temperature, although included in the best-fitting model, was not a significant predictor of group size. The total variance explained by the random effects in this final GS model was low ($3.48\ \mathrm{E}^{-08}$), with 8.5% contributed by phylogeny, and 91.5% contributed by inter-population (within-species) variation. Again, there was concordance between this best approximating model and the parameters derived by the model-averaging approach (using the 95.7% confidence model set) in terms of coefficient relative magnitude and significance, with mating system and annual precipitation still the only significant terms and each having high RI values (1.00 and 0.87 respectively; Table 5.7). As such, the top-ranked GS model likely represents, by parsimony, the best model obtainable for the data, and a valid best approximation of the observed patterns.

For the best-approximating HR and GS models, an assessment of model fit supported the validity of these final models. Examination of observed HR values compared to those predicted by the top-ranking model confirmed a linear trend (Figure 5.2 a)), indicating that specification of main effects only did not result in poor fit due to omission of any major interaction terms, and that the mixed effects linear model derived is adequate. A similar pattern, though not as neatly linear, was evident for the observed versus predicted GS values from the best-ranking model (Figure 5.2 b)), thus supporting this model as a plausible and valid representation of the data. Plots of residuals versus predicted values from each model further confirmed the adequacy of both models, with points scattering about zero (indicated by line at $y = 0$) and no obvious linearity or curvature apparent (Figure 5.2 c) and d)). For fitted HR, although higher values of HR showed small residuals, this is likely due to a smaller number of observations of large HR, and there was no systematic pattern of departure from zero, with both high and low HR values showing positive and negative residuals, and low values showing both large and small residuals. There was also no obvious pattern of residual dependence on the predicted GS, with no greater residuals apparent for higher GS values than low, and positive and negative residuals for all values of GS. In each plot exploring HR and GS model fit, the small cluster of four points occurring at higher HR and GS values correspond to four *Nomascus* populations from three closely related species: two populations of *N. concolor*, and each single surviving population of *N. hainanus* and *N. nasutus*. The residual plots do not reveal the larger HR and GS values observed for these *Nomascus* populations to be strictly outliers, but they are sitting as a slightly separated cluster, highlighting that they are uncommon, but are explained by the models as evident by the linear patterns.

Mating system was not explained by any potential intrinsic or extrinsic predictor variables, whether tested in single predictor regression models, or together in an exploratory global model combining all 13 potential predictors (Table 5.8). The variance explained by phylogeny for the random effects was infinite, indicating a strong effect of between-species phylogenetic relationships relative to within-species variation. As no significant fixed effects predictors were detected, no further analysis of this response variable was possible within the scope of this analysis.

Table 5.4 Fixed effects parameter estimates for HR: best-approximating linear mixed-effects kinship model incorporating phylogenetic and within species variance-covariance fit by maximum likelihood (residual error: 0.113). Model fitting incorporates both fixed and random effects in parameter estimates, *P*-values less than 0.05 are **emboldened**.

Coefficient	**Estimate**	**SE**	**z-value**	***P*-value**
(Intercept)	1.03	0.22	4.66	**3.10E-06**
group density	-0.14	0.04	-3.19	**0.001**
mating system (1=polygyny)	0.30	0.11	2.58	**0.010**
group size	0.99	0.40	2.49	**0.013**

Table 5.5 Model-averaged fixed effects parameter estimates for HR (from n=19 model set with ΔAICc<7 and cumulative $w_i > 0.95$), with relative importance (RI) of each parameter, *P*-values less than 0.05 are **emboldened**.

Coefficient	**Averaged estimate (β)**	**SE**	**z-value**	***P*-value**	**RI**
(Intercept)	1.35	0.58	2.33	**0.020**	NA
group density	-0.13	0.05	2.58	**0.010**	0.70
group size	1.22	0.50	2.44	**0.015**	0.84
mating system (1=polygyny)	0.33	0.15	2.22	**0.026**	0.83
annual mean temperature	-0.02	0.01	1.51	0.132	0.43
annual precipitation	-0.19	0.17	1.08	0.282	0.26

Table 5.6 Fixed effects parameter estimates for GS: best-approximating linear mixed-effects kinship model incorporating phylogenetic and within species variance-covariance fit by maximum likelihood (residual error: 0.045). Model fitting incorporates both fixed and random effects in parameter estimates, *P*-values less than 0.05 are **emboldened**.

Coefficient	**Estimate**	**SE**	**z-value**	***P*-value**
(Intercept)	0.98	0.18	5.55	**2.80E-08**
mating system (1=polygyny)	0.22	0.03	6.85	**7.20E-12**
annual precipitation	-0.16	0.06	-2.96	**0.003**
annual mean temperature	0.005	0.003	1.59	0.110

Table 5.7 Model-averaged fixed effects parameter estimates for GS (from n=10 model set with ΔAICc<7 and cumulative $w_i > 0.95$), with relative importance (RI) of each parameter, P-values less than 0.05 are **emboldened**.

Coefficient	**Averaged estimate (β)**	**SE**	**z-value**	***P*-value**	**RI**
(Intercept)	0.94	0.23	4.03	**0.0001**	NA
mating system (1=polygyny)	0.21	0.03	6.29	**<2.00E-16**	1.00
annual precipitation	-0.15	0.06	2.63	**0.009**	0.87
annual mean temperature	0.005	0.003	1.43	0.153	0.39
latitude	-0.001	0.001	0.48	0.634	0.22

Table 5.8 Exploratory global multiple regression model for MS; linear mixed-effects kinship model incorporating phylogenetic and within species variance-covariance fit by maximum likelihood (residual error: 0.129), with all possible putative fixed effect predictors, P-values less than 0.05 are **emboldened**.

Coefficient	**Estimate**	**SE**	**z-value**	***P*-value**
(Intercept)	0.34	0.16	2.07	**0.039**
group size	1.36	0.50	1.86	0.063
home range	0.50	0.23	1.82	0.069
NDVI	-0.59	0.30	-1.79	0.073
altitude	0.16	0.10	1.72	0.085
reserve area	-0.06	0.03	-1.66	0.097
species adult body weight	0.45	0.33	1.38	0.170
GHF	-0.32	0.31	-1.03	0.310
annual precipitation	-0.18	0.24	-0.73	0.460
precipitation seasonality	-0.27	0.37	-0.74	0.460
latitude	0.00	0.01	0.37	0.710
longitude	0.00	0.01	0.28	0.780
annual mean temperature	0.01	0.03	0.24	0.810
group density	0.02	0.08	0.22	0.830

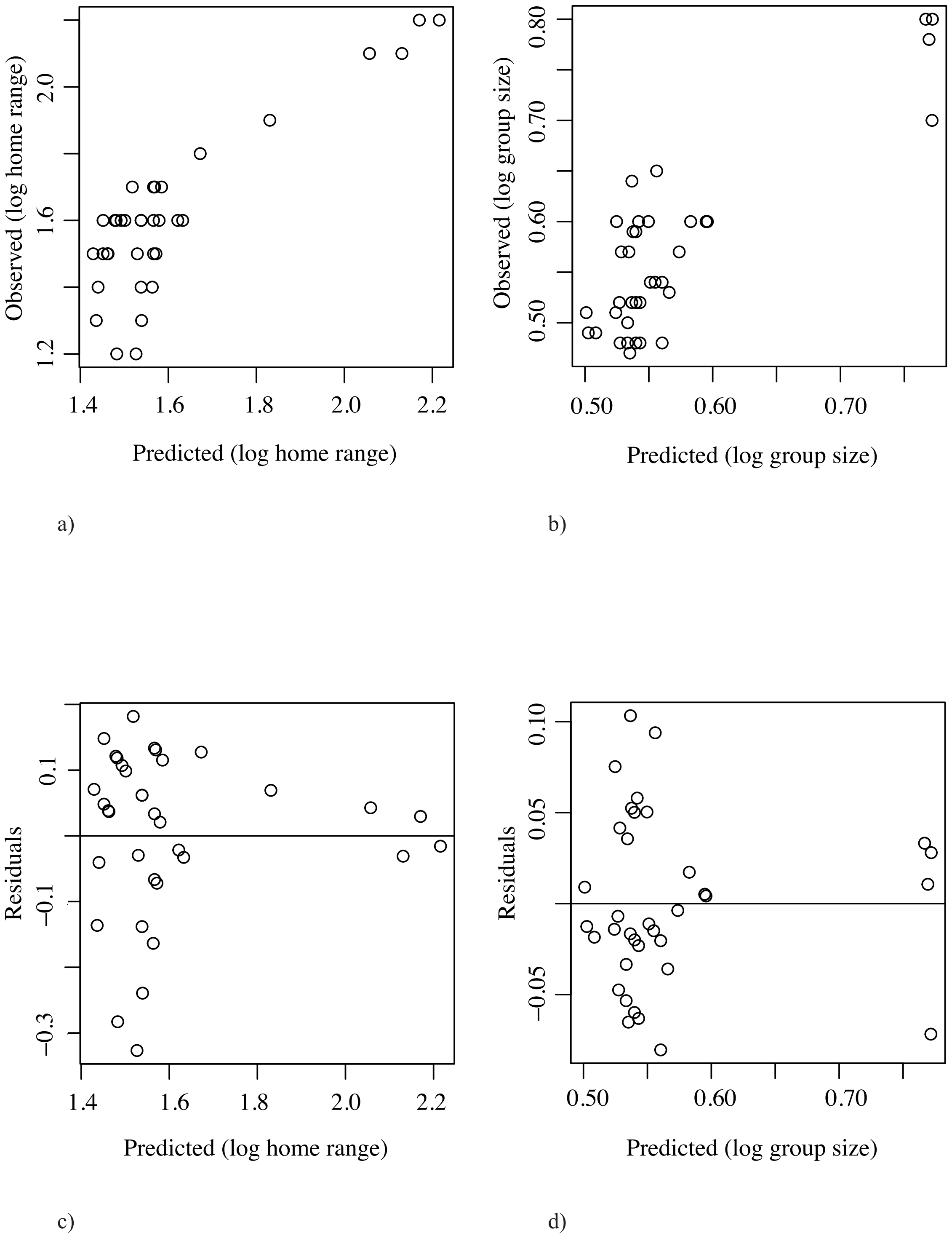


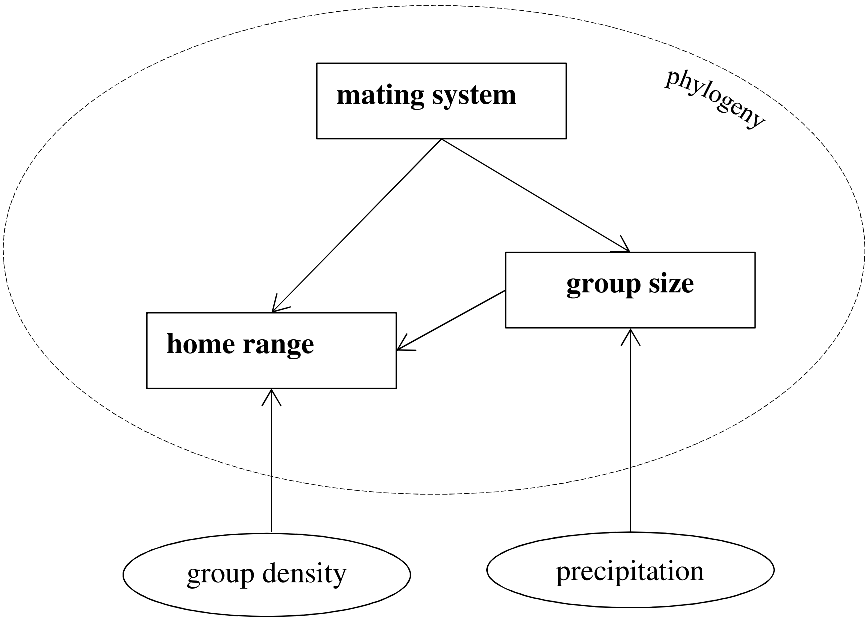
Figure 5.2 Scatterplots of model fit: a) observed HR values (log-transformed) versus values predicted under best-approximating linear mixed-effects kinship model for HR (log values); b) observed GS values (log-transformed) versus values predicted under best-approximating linear mixed-effects kinship model for GS (log values); c) HR values predicted under best-approximating linear mixed-effects kinship model for HR (log values) versus model residuals; d) GS values predicted under best-approximating linear mixed-effects kinship model for GS (log values) versus model residuals.

Discussion

Drivers of family-wide trait patterns

This study represents the first known assessment of trait patterns within the Hylobatidae using the most recent advances in comparative analysis. While a small number of studies have indicated phylogenetic signals for selected behavioural and ecological traits in primates, including mating system (Opie et al. 2012), group size and home range (Kamilar and Cooper 2013), this work presents new evidence of such phylogenetic trait-association in gibbons. A strong, significant phylogenetic signal was detected for home range, group size and mating system, indicating that these traits are phylogenetically conserved within the family. By accounting for this strong phylogenetic structure, and incorporating additional intra-species variation, the predictive analyses revealed additional intrinsic and extrinsic factors which explain the variation observed in gibbon ranging requirements and social structure. It is apparent that gibbon mating strategy, group size and home range are inherently linked, with these factors being important, inter-correlated predictors of each other, along with a limited number of site-level factors (Figure 5.3). Thus, a combination of social dynamics and external factors seem to drive variation in these traits within the family.

Figure 5.3 Detected drivers of HR and GS in gibbons: relationship between response variables investigated showing inter-connectivity of HR, GS and MS as apparent drivers, as well as responses, along with two site-level extrinsic drivers.



Home range

Two intrinsic factors explained variability in home range across gibbon populations: mating system and group size, which were also linked. The positive association of home range with group size aligns with broader patterns seen across the primates. As larger groups will more rapidly deplete food sources in discrete patches (e.g. known food trees), they must range further within a day and thus across a year to satisfy the greater energy requirements of a larger group, leading to larger overall home ranges (Wrangham et al. 1993, Chapman and Chapman 2000, Gillespie and Chapman 2001). Therefore, for gibbons, despite the advantage gained by their energy-efficient locomotion (brachiation), it seems that larger groups are still associated with larger home ranges. Polygynous populations were also linked to larger home ranges. As polygynous groups form larger groups, it is likely this is an associated effect, as per the relationship detected between these two traits (see below).

Accounting for mating system and group size, those sites with lower group densities were concomitant with larger home ranges. Therefore, it seems that populations with fewer neighbouring groups are more likely to exhibit larger home ranges. This provides some indirect evidence for a ‘disturbance’ effect, with low group densities generally more likely to occur in more threatened species (as a result of low population sizes). Notably, those *Nomascus* species showing the largest home ranges in the family, the sister species *N. hainanus* and *N. nasutus* and the closely related *N. concolor*, were found to be exhibiting more extreme home range values than predicted according to phylogenetic dependence alone. The population sizes and thus densities of these species are greatly reduced (Fan et al. 2006, Mootnick et al. 2012). These lower group densities, along with larger polygynous groups observed for the four populations of these species incorporated in the analyses, could explain these more extreme home range values. Within-species variation in gibbon density has been shown to correlate with site-level vegetation parameters. For example, higher group densities in *Hylobates albibarbis* are positively associated with canopy cover, tree height, density of large trees and the availability of food trees in the Sabangau Catchment, Indonesia (Hamard et al. 2010), and a number of studies have found a strong positive association between the availability of preferred food trees and gibbon densities (Mather 1992, Marshall and Leighton 2006, Marshall 2009, Chivers 2013). Ultimately, this may mean that site carrying capacity may drive home range through site-level resource availability dictating group density, although further investigation of what determines group density at different scales will clearly be crucial to understanding the ultimate drivers of home range size. Nevertheless, the correlates revealed here allude to both intrinsic and site-level extrinsic drivers of home range size across the Hylobatidae.

Group size

The predictive model revealed variation in gibbon group size to be linked to social and climatic drivers. Larger group sizes were associated with a polygynous mating system and low mean annual rainfall. Polygynous groups will by their nature have more members than monogamous groups, so this significant effect is not surprising, but this analysis confirms that it is a key driver of group size variation in the Hylobatidae. Larger group sizes were also more likely at sites with lower annual precipitation levels. Drier areas predicting larger groups initially seems counterintuitive, as it is generally thought that habitats with higher levels of annual rainfall will have higher productivity and thus be richer in resources than drier habitats in tropical forests (Richards 1996). However, Kay et al. (1997) demonstrated that tropical forest productivity declines when annual rainfall exceeds 2,500mm, likely due to nutrient leaching depressing plant growth. Therefore, patterns of increased precipitation within the moist tropical habitats primarily inhabited by gibbons may have a negative impact upon the growth of required gibbon food trees. Indeed, tree density and primate biomass have been shown to decline with increasing rainfall levels in Southeast Asian forests (Gupta and Chivers 1999), and frugivorous primate biomass specifically declines with greater annual rainfall in Asian tropical forests (Janson and Chapman 1999). So, across those gibbon populations sampled (annual precipitation range: approximately 1,100-4,000mm), drier sites may be relatively richer in terms of available resources. Such increased resource availability could permit larger group sizes (driven by mating system) by reducing intra-group feeding competition, which is recognised as the major cost of group living among primates and thus thought to regulate group size (van Schaik 1983, Wrangham et al. 1993, Janson and Goldsmith 1995). The proxy for productivity tested (NDVI) did not significantly explain group size variation; however, this may be due to insensitivity of this metric to capture fine-resolution differences in food loads in tropical forests rather than the absence of a relationship *per se* (see further discussion below). It therefore remains to be determined if the relationship between group size and rainfall belies an association with productivity and/or food availability. Regardless, the rainfall correlate alone indicates the influence of an extrinsic factor on this trait, but one that is fundamental to the resource capacity of a site and unlikely to signal any direct effect of site disturbance at present.

Mating system

Beyond a strong phylogenetic signal, there were no explanatory variables statistically associated with mating system, and therefore no evidence of any other intrinsic or extrinsic factors accounting for the variation in this trait seen across the Hylobatidae. It seems unlikely that this is solely the result of limitations associated with the analytical approach. While the predictive power of a binary response model may be low, Grafen and Ridley (1996) demonstrated that phylogenetic regression is valid and robust for binary response variables. It is more likely that the results indicate genuine poor support for (recent) extrinsic factors driving the observed variation in mating system, and the present patterns are the result of longer-term evolutionary processes. Using Bayesian phylogenetic models to investigate the evolutionary history of mating systems in primates, Opie et al. (2012) estimated that monogamy may have evolved in the gibbons approximately 19mya. While these authors did not incorporate fine-scale patterns of variation within the Hylobatidae, they did demonstrate that across primates, monogamy evolved from polygyny, with a strong transition rate in this direction and a zero reverse rate. This supports polygyny as an ancestral state for this trait and thus a low likelihood of this form of mating system being manifest by populations as a recent response to compromised habitat conditions. It is therefore perhaps unsurprising that there was no direct evidence for any current-condition extrinsic factors associated with this trait, including those meant to capture site condition (NDVI, GHF). To detect the ultimate drivers of mating system, including any causal mechanisms of possible within-family plasticity, it would thus be necessary to incorporate data on historical environmental conditions. However, elucidating such evolutionary drivers was not the focus of this study, and there is already a wealth of literature discussing the possible ultimate causes of monogamy in gibbons. Proposed mechanisms include: female intra-sexual aggression to secure a mate and reduce infanticide risk (van Schaik and Dunbar 1990, Palombit 1999, van Schaik and Kappeler 2003); inability of males to monopolise more than one breeding female due to female dispersion (van Schaik and van Hooff 1983, Brockelman and Srikosamatara 1984) and energetic constraints imposed by territoriality (Bartlett 2009); and fitness advantages to males (e.g. lower cuckolding risk) (Leighton 1987, Reichard 2003). Despite this, none of the proposed explanations has convincingly demonstrated a causal link to monogamy in gibbons (Reichard 2003). Future work using techniques which were beyond the scope of this analysis, including evolutionary trait mapping and ancestral character reconstruction, could therefore be helpful in clarifying both the evolutionary drivers of and apparent flexibility in mating system in the Hylobatidae.

Limited evidence for a disturbance hypothesis

A fundamental concept in behavioural ecology is that animals will show behavioural responses first to changes in their environment, with adaptations in life history, physiology and morphology occurring over longer periods (Relyea 2001). It follows then that gibbons may show flexibility in key behavioural traits in response to external factors, including recent habitat changes due to human disturbance and degradation. In this study I found evidence for intrinsic and extrinsic drivers of gibbon ranging requirements and social group size, but only limited support for any association with site disturbance or quality. Home range variation was explained by group density at a site, indirectly indicating a possible effect of carrying capacity, and thus response to habitat conditions. However, group size was linked to a climatic variable that is unlikely to herald any disturbance impact at present (although this factor may become important in the near future under projected climate change scenarios). Similarly, I found no direct support for the disturbance-hypothesis explanation for mating system.

None of the traits were statistically linked to the proxies employed to represent site habitat productivity/quality (NDVI) or disturbance (GHF). However, this lack of association may be due to the limitations of these metrics. NDVI is derived from a two-dimensional representation of vegetation cover (satellite images) and therefore may saturate in high biomass areas, making NDVI values insensitive to increasing vegetation (Hobbs 1995). Consequently, when comparing across high biomass areas such as tropical forests, where differences in biomass are likely to correspond to below-canopy differences in vegetation mass, NDVI may not be sufficiently resolute to capture heterogeneity at finer scales. Similarly, although the scale of the GHF metric may have been appropriate (1 km resolution), the measure may have failed to capture the human impacts of greatest importance to gibbon populations. This measure incorporates global data on human disturbance (population density, land use, infrastructure, cadastral features), but does not include key human impacts to gibbons, namely localised hunting and small-scale forest alteration. Therefore, the impact of disturbance may be underestimated by this metric. Unfortunately, despite efforts to obtain such data (via a direct survey of researchers), for site-level information it was necessary to adopt these metrics in the absence of robust, standardised, fine-scale data on site disturbance.

A further consideration is that there may be other variables not included in the analyses that may explain the variation of these traits in gibbons. This is a principal limitation in predictive modelling; models will only provide information about those variables incorporated in the analyses, and nothing about any potential relationships for those variables not included. However, parameter-saturated models will suffer from over-parameterisation and have no explanatory power, i.e. no degrees of freedom (Harrell et al. 1985, Crawley 2007), therefore not all possible variables can be tested. I attempted to circumvent both of these issues by selecting putative predictors for which there was *a priori* reasoning for a relationship. Therefore, while it is not possible to completely rule out a disturbance-associated effect to explain the notable variations seen in the behaviour and ecology of some gibbon populations, beyond the insights into home range, the evidence obtained within this study for such an explanation is limited.

Possible limitations of the analyses

Potential caveats to the phylogenetic analyses include tree size and structure. The incorporated phylogenetic tree contained only 21 tips (19 gibbon and two *Pongo* species). Pagel's λ may have low power when the number of tips is small; however, simulations have shown phylogenies of this size (c.20 species) are more likely to be subject to type II than type I errors

(Freckleton et al. 2002, Münkemüller et al. 2012), meaning that false signals are unlikely. Furthermore, the phylogenetic signals detected were all close to λ=1, indicating strong phylogenetic structure in these continuous variables, even in the absence of any thresholds applied for statistical significance. This included the control variable (body weight), for which a strong signal was expected, and found, indicating the validity of the results for all variables. Similarly, small tree sizes and high or low trait prevalence (proportions of one character state), as seen here, may prevent detection of a phylogenetic signal in binary traits tested via *D*, but again this should not produce significant signals where there are none (Fritz and Purvis 2010). The large value of *D* detected for the binary variable also enhances our confidence in the accuracy of the result.

Inaccuracies associated with phylogenetic inference must also be considered. It did not prove possible to utilise alternative phylogenies or alternative tree topologies to incorporate such uncertainty. Phylogenies proposed prior to that of Thinh et al. (2010a) do not include many of the more recently designated species, or complete data on divergence dates, and so were not appropriate to use. Furthermore, the small dataset prevented the use of more advanced methods to derive alternative tree topologies (e.g. via phylogenetic estimation resampling). In practice, however, uncertainty captured by such subtle variations to tree topology may have little impact upon the correlation matrix derived from the phylogeny for comparative tests (Paradis 2011), and recent simulations indicate that λ is relatively robust to tree uncertainty and tree size when signal strength is strong (Münkemüller et al. 2012). Consequently, the significant phylogenetic signal detected for all three traits is unlikely to be a result of any constraints to tree size or uncertainty in structure.

The existence of only 19 gibbon species fundamentally constrained the sample for the predictive modelling. This was further compounded by the fact that only a small number of populations of most species are well-studied, limiting the number of populations for which robust, empirical data could be incorporated. Even for some well-known populations, data access was restricted by lack of access to unpublished documents and concerns regarding data sharing within the research community. As such, the representativeness of the final data set may be reduced. However, this analysis combined information from almost 40 populations of all 19 currently recognised gibbon species, and is a novel approach using advanced comparative methods to investigate trait patterns across the Hylobatidae, based upon the most comprehensive collection of population-level gibbon data available to date. Nevertheless, this study constitutes a preliminary analysis of the potential intrinsic and extrinsic drivers of these traits, and further analyses incorporating finer-resolution data and additional populations, if possible, could serve to clarify possible additional correlates, including human-induced habitat disturbance and degradation.

Implications for Hainan gibbon management

In the context of the existing paradigm of gibbon ecology and behaviour, the Hainan gibbon has been regarded as displaying unusual patterns of home range and social organisation. These reputed anomalies have been rationalised through disturbance impacts, including reduced habitat availability and quality within BNNR, and/or small population size limiting mate availability and thus social group formation and altering group structure (Bleisch and Chen 1991, Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b). This comparative analysis signifies the first attempt to formally contextualise the species' behavioural and ecological patterns within family-wide variation in these traits, to try to identify associated intrinsic and extrinsic factors and so ascertain if the species is indeed unusual. The analyses conducted have appreciable limitations, but nevertheless the results provide important new insights into the biology of the Hainan gibbon.

I found evidence that the Hainan gibbon, along with populations of the closely related and similarly Critically Endangered species *N. concolor* and *N. nasutus*, exhibit home ranges that are larger than expected relative to other gibbon species, according to the strong phylogenetic signal that exists for this trait within the Hylobatidae. Such extreme values may either point to different rates of evolution for these taxa (as basal *Nomascus* species) compared to the rest of the family, or the influence of other, non-phylogenetic factors. Through increased analytical resolution, the predictive models provided support for both intrinsic and extrinsic drivers of this pattern: low group density in combination with a polygynous mating system and larger group size were correlates of larger home ranges. This association indirectly indicates a possible disturbance effect, in that gibbon population density and group density within BNNR are critically low, and lends support to the theory that Hainan gibbon home ranges may be expanded as a result of a lack of adjacent groups (Fellowes et al. 2008). This apparent plasticity must be taken into account when considering potential management actions, even simply in terms of predicting the possible response of the population to measures such as increasing the available habitat. Whether the quality of the available habitat also contributes to the large spatial requirement in the Hainan gibbon will require further, focused investigation. However, the lack of direct correlation of home range with productivity (NDVI), as a metric of site condition, would indicate that actions designed to improve habitat quality and availability alone will be unlikely to address the current constraint on Hainan gibbon population recovery. This is not to suggest that these factors may not positively impact the population, or that efforts to protect and enhance the BNNR landscape should not be continued, but rather that more intensive management actions may be required to enhance the species' population growth.

In comparison, Hainan gibbon group size was not found to be more extreme than that predicted under full phylogenetic structure, for which there was a strong signal within the family.

Furthermore, hylobatid-wide variation in group size was best explained by the species' mating system and site annual precipitation levels. Thus, there was no support for the large size of Hainan gibbon groups being directly linked to any site disturbance issues. Instead, these results indicate an underlying flexibility in this behavioural trait across the Hylobatidae driven by both intrinsic and extrinsic factors, but not those immediately associated with recent habitat degradation. Beyond a tendency for mating system to be phylogenetically determined, insights into the possible mechanisms behind the manifestation of polygynous gibbon groups were limited. The fact that none of the predictor variables designed to capture site condition showed any association with mating system limits confidence in the theory that polygyny in the Hainan gibbon is displayed in response to poor habitat, although detection of such a pattern for any of the traits may require more fine-scale data on these aspects than it was possible to include here. Together, these results suggest that large, polygynous groups may be the normal structure for Hainan gibbon social groups. This has important implications for the conservation management of the population. First, these traits are not likely to be reliable indicators of the condition of the population, as a result of present human impact or any change in condition that might be expected under possible management scenarios. Second, any potential actions, for example translocation of part of the population to establish a second population, must take into account the complex, polygynous social structure of the species as part of its intrinsic biology that must be accommodated. This is a crucial new insight that will directly impact Hainan gibbon conservation.

Chapter 6. Hanging in there? Population viability analysis of the last population of the Hainan gibbon

Introduction

A complex combination of extrinsic and intrinsic factors can influence the demographic growth rate of a wild population and ultimately depress this rate such that the population declines (Tarsi and Tuff 2012). Understanding the influence of each of these factors and how they interact is vital to successfully managing a population of a threatened species (Soulé 1985). External drivers of population decline (e.g. habitat destruction, over-harvesting, invasive competitors and/or predators, pollution) are largely deterministic in their nature; they generally have a consistent and predictable effect upon population growth rates, shifting species from long-term average population growth to decline (Lacy 1993-1994). Given sufficient resources, political commitment and on-site support, under certain circumstances, identification and management of such deterministic causes of species decline can have a meaningful impact. For example, populations of kokako (*Callaeas cinerea wilsoni*) in forests where introduced predators were intensively controlled have rapidly recovered, trebling in number in just eight years at one site (Innes et al. 1999). However, for exceptionally small populations of threatened species, like the Hainan gibbon, additional factors must be considered in order to accurately understand the population's extinction risk and thus adequately plan for the species' conservation.

As a population declines, it can suffer additional deterministic effects (e.g. Allee effects) and, crucially, becomes subject to further stochastic factors that can vary greatly in terms of the magnitude and direction of their impact. These factors have only a minor influence in large populations as their size lends an overall robustness to such fluctuations, but the same stochastic processes play a major role in determining the fate of small populations. As Caughley (1994) outlined, the dynamics of a large population are governed by the law of averages, while those of a small population are governed by the specific fortunes of its few individuals. In a small population, instability is added by the influence of four forms of stochasticity: demographic, environmental, and genetic stochasticity, and catastrophes (Shaffer 1981). These stochastic effects can interact with and add to deterministic effects to lead to a further reduction in population size, which may further increase the instability of the population. This increased instability can result in yet further decline in population size, driving populations ever downward in a cycle to extinction: the 'extinction vortex' (Gilpin and Soulé 1986). This relationship between population size and extinction risk has been recognised theoretically since the work of Shaffer (1987) and Lande (1993), but recent work by Fagan and Holmes (2006), involving analysis of a time-series dataset for extinct populations of ten vertebrate species, has empirically demonstrated that wild populations do experience accelerating susceptibility to extinction as they decline, with the time to extinction becoming exponentially smaller as populations diminish.

It is clear that for small populations of threatened species, even if the initial, deterministic causes of the decline of a population are known and can be controlled, it may be the inherent instability in the population caused by stochastic forces that will result in the final loss of the species (Shaffer 1981, Soulé 1987). For example, a remnant population of greater prairie chickens (*Tympanuchus cupido pinnatus*),which initially declined as a result of habitat loss and fragmentation, continued to decline, despite reforestation efforts, due to inbreeding depression within the population suppressing reproductive rates (Westemeier et al. 1998). It was ultimately the genetic stochasticity of the population that prevented its recovery. Therefore, it is essential to consider and address the individual and combined impacts of extrinsic deterministic factors and the stochastic effects intrinsic to the dynamics of a small population if we are to attempt to reduce a species' risk of extinction (Caughley 1994).

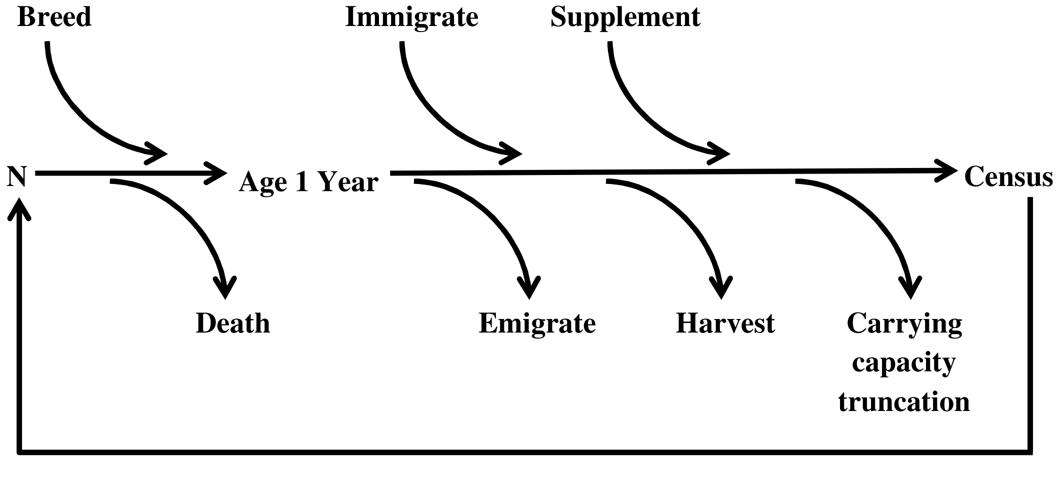
Despite identification of both deterministic and likely intrinsic threats to the species' survival (Liu et al. 1989, Chan et al. 2005, Fellowes et al. 2008), there has been no attempt to investigate the probable impact of this suite of factors upon the tiny remnant population of the Hainan gibbon. As such, it is not possible to accurately understand the likely viability of the species in its present situation. To improve our understanding of the probable fate of the species in the context of this complex combination of factors, I aimed to assess the viability of the sole persisting Hainan gibbon population by conducting a Population Viability Analysis (PVA). PVA is an analytical tool that incorporates the combined effects of deterministic and stochastic factors to assess the likelihood that a population will persist for a given time into the future (Gilpin and Soulé 1986). PVA is widely used to identify and evaluate possible threats, predict the likely fate of populations, and estimate the relative probability of extinction of a species under different potential scenarios (Akçakaya and Sjogren-Gulve 2000). Model projections can also be used to assess and rank potential management actions, making PVA an invaluable tool, as managers often lack, but highly value, information that will help them prioritise management options (Cook et al. 2012). This type of investigation is particularly important for the Hainan gibbon, where the population size is critically low, but also where substantial cultural, logistical and political barriers will likely affect the implementation of management actions, as has been the case for conservation of other Chinese mammals (Schaller 1993, Turvey 2008). Consequently, objective identification of priorities for conservation management is vital.

Through PVA I aimed to determine the viability of the sole remaining Hainan gibbon population under current conditions in BNNR, identify key intrinsic factors that have the greatest influence on Hainan gibbon population growth rates and viability, and explore the impact of key extrinsic threats upon viability to identify the drivers of Hainan gibbon extinction risk. In addition to this principal objective of determining the likely outcome of taking no action to conserve the species (status quo), I also aimed to determine the relative viability of the population under two potential management scenarios. This fundamental investigation was intended to provide insights into the likely outcomes of these possible conservation actions and thus their relative ability to improve the species' chances of survival. This viability analysis therefore contributes a crucial evidence-base relevant to best-practice conservation planning required to conserve the species.

Methods

I explored the viability of the remaining Hainan gibbon population using VORTEX V.9.99c (Lacy 1993). VORTEX is a Monte Carlo simulation program that models the combined effects of deterministic forces and stochastic events (demographic, environmental, genetic and catastrophes) on small populations by simulating population dynamics as discrete sequential events that occur according to defined probabilities (Lacy 2000, Miller and Lacy 2005). Each individual is tracked as the simulation steps through life cycle events (e.g. births, deaths, catastrophic events; Figure 6.1), with growth checked by truncation to the specified carrying capacity ('*K*'). VORTEX is appropriate for modelling the Hainan gibbon population as it is designed specifically for mammalian and avian populations with low fecundity and long life spans. As there are limits to the complexity with which VORTEX can represent a situation, a certain amount of simplification was required when developing simulation models.

Figure 6.1 Cyclic sequence of demographic events within VORTEX PVA simulation (after Miller and Lacy 2005). Events are modelled by determining whether any of these events occur for each animal in each year of the simulation as it progresses through generations. Events above the timeline increase N, while events below decrease N.



Baseline model

The null or 'baseline' model was designed to represent the Hainan gibbon population as it is presently understood to persist. No threatening processes, beyond the demographic and stochastic effects of a small population size (including inbreeding), were incorporated into this model. It therefore provides insight into the probable population trajectory and viability of the species under the optimistic assumptions that the species is no longer vulnerable to such threats as hunting and habitat loss, and may be so fortunate as to avoid catastrophic events. Fundamentally, this model allows us to predict the probable outcome of failing to implement any conservation management actions (even in the absence of threats).

I selected input values for the demographic variables within the baseline model using available information from the literature and that gathered during this study (see Chapters 3-5). Very few life-history data are available for the species, so most information was taken from early observations by Liu et al. (1984, 1987, 1989), and revised using more recent data (Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b, Li et al. 2010). Values were appropriated from closely-related gibbon species for those input variables where data were unavailable for the Hainan gibbon, with precedence given to data from wild gibbon populations over captive, and data from *Nomascus* taxa whenever possible.

General model settings

Unless otherwise stated, I simulated one isolated initial population of 25 individuals, using 1,000 iterations for each scenario, over a simulation period of 150 years. This time period corresponds to approximately 10 gibbon generations (generation time: 15 years; Chivers et al. 2013), as is appropriate to simulate long-term trends by allowing the processes modelled to influence projections of population dynamics in this relatively long-lived species. I included concordance between environmental variation in reproduction and survival, meaning good years for survival in the simulation were also good years for reproduction, as can be expected for wild populations. I specified inbreeding within the population (Frankham et al. 2014) and used a detailed pedigree I developed from field observations and genetic analyses (see Chapter 3) to more accurately incorporate relatedness of individuals and effects of inbreeding. Adopting the pedigree also allowed me to detail the structure of the starting (existing) population in terms of age and sex distribution. Ages and sexes of unknown individuals (predominantly solitary individuals) were estimated based upon likely ages of gibbons post-dispersal, observations of one sexually-maturing female (a single encounter of a female mid pelage colour transition), and detected calling behaviour of at least one adult male. 'Extinction' was defined in every scenario as the absence of one sex in the simulated population.

Demographic sensitivity testing

To investigate uncertainty surrounding the baseline input values, I carried out demographic sensitivity testing. This involves modelling a range of values for a given input parameter to assess the impact of imprecision in that variable on the precision of model projections. Crucially, it therefore also reveals the sensitivity of the model to the different model parameters, indicating which factors are key in determining Hainan gibbon population dynamics, and thus which demographic variables have the greatest influence on the ultimate viability of the population. Variables were only varied within biologically meaningful limits. As such, the relative ranges of values tested for each demographic variable were not equal; most values were altered by 20-50% (increase or decrease), but to capture the feasible values for some demographic variables it was necessary to increase the baseline value by more than 300% (e.g. mortality at dispersal age). This range of values tested was taken into account when assessing the sensitivity of the model to the demographic variables. Explanation and justification of the individual values for each input parameter used within the baseline model and demographic sensitivity testing can be found in Appendix L. Input parameter values used in the baseline model and value ranges explored via sensitivity testing are summarised in Table 6.1.

Table 6.1 Parameter values for demographic variables used in baseline VORTEX PVA model of Hainan gibbon population dynamics, with range of values assessed via sensitivity testing.

Input parameter	**Value**	**Sensitivity testing (value range)**
No. of populations	1	n/a
Initial population size	25	n/a
Genetic management	Initial population pedigree	n/a
No. of iterations	1000	n/a
No. of years	150	n/a
Extinction definition	Only 1 sex remains	n/a
Stable age distribution	No, specified by pedigree	n/a
Inbreeding depression	Yes	n/a
Lethal equivalents	6	3.14, 12
Reproductive system	Long-term polygyny	n/a
Age of first offspring for females	8	10
Age of first offspring for males	10	8, 12
Maximum age of reproduction	30	26, 28, 32
Maximum no. of broods/year	1	n/a
Maximum no. of progeny/brood	1	n/a
Sex ratio at birth (% males)	50	65, 75
Adult females breeding (%)	(2 year IBI) 50	(3 year IBI) 33
EV in % females breeding	5 (=10%)	10, 15, 20 (=20%, 30%, 40%)
Mortality (%) age 0 to 1 (infant)	10 (SD=2)	15 (SD=3), 20 (SD=4)
Mortality (%) age 7 to 8 (dispersal)	25 (SD=5)	15 (SD=3), 30 (SD=6), 50 (SD=10)
Mortality (%) all other age classes	5 (SD=1)	n/a
Males in breeding pool (%)	100	70, 80, 90
Carrying capacity ('*K*')	30	50, 65, 80
Harvest	none	n/a
No./type of catastrophes	none	n/a

Incorporating threats and catastrophes

Despite ongoing efforts to protect the species, the population remains vulnerable to anthropogenic threats and risk of environmental catastrophes, and it is important to determine the impact these processes will have upon population viability. Therefore, I developed separate models from the baseline model to explore the impact of two known threats and the risk of catastrophe. I explored each threat at varying levels to understand the individual consequences of the threat in increasingly adverse situations. In reality, several threats are likely to be acting upon the population at once, but I initially modelled feasible threats in isolation to assess the relative, individual influence of each threat upon the population's viability, before combining them. These models therefore represent comprehensive investigation of the consequences of taking no conservation actions, so retaining population at status quo, under the more likely scenario/s that the population is vulnerable to various threats.

Hunting

Historically, the Hainan gibbon was intensively hunted across Hainan for Traditional Chinese Medicine (Chan et al. 2005), with acute hunting still occurring in the 1970s despite an already greatly restricted population (Zhang et al. 1981, Liu et al. 1984). In 1988, it become illegal to hunt the species following its classification as a Class I Nationally Protected Species under the Chinese (Wildlife Protection Law Government of the People's Republic of China, 1988). Since the early 2000s, there has been intermittent patrol monitoring of the population affording it some protection, and efforts to improve local attitudes through awareness raising and community education activities (Fellowes et al. 2008). There have been no known hunting events since those reported in the early 1990s (Zhang 1992, Zhang and Sheeran 1993), but anecdotal reports suggest at least one possible unreported hunting event occurred in the last 15 years (approximately 2002-2003; Bosco Chan pers. comm., March 2014). Even with the compliance of the majority of inhabitants of villages surrounding the reserve, the population is still at risk from hunting, both directly and indirectly. Gibbons may be hunted deliberately by outsiders or intruders, or accidentally by local villagers seeking other (similar-sized) arboreal mammalian prey (Chan et al. 2005), e.g. black giant squirrel (*Ratufa bicolor*), Hainan giant flying squirrel (*Petaurista hainanus*).

To investigate the impact of this potential threat upon the population's fate, I modelled a scenario in which individuals were poached from the population by specifying the removal ('harvest') of one adult male-female pair every ten years over the simulated period. This equates to roughly a 5% chance of an individual being hunted in a given year. This is an arbitrary estimate in the absence of any data on the potential risk of hunting, as this type of data is particularly difficult to collect for any population. As larger animals are likely to be more conspicuous in the landscape, the removal of adults over juveniles and infants is realistic. Specification of a 'pair' of gibbons was necessary as it was not possible to specify alternating sexes in alternative years, or to randomise probability of a particular sex being hunted each year for losses of single individuals. As males and females are both visually conspicuous and thus likely have equal risk of being hunted, it was important to incorporate loss of both sexes. To explore a greater risk of hunting, should the arbitrary value set be an underestimate, or should regular hunting or removal of animals increase for whatever reason, greater frequencies of pair removal were also simulated: one pair every five years, every two years, every year. This exploratory model incorporating hunting pressure was meant as a simple representation of the threat of hunting.

Habitat loss

Given the highly restricted amount of habitat available to the population, additional habitat loss is likely to have important consequences for the viability of the population. Despite a ban on commercial logging in Hainan Province since 1994 (Chan et al. 2005), vast tracts of prime gibbon habitat have continued to be lost, predominantly in low-elevation areas. In particular, Zhang et al. (2010) reported a 7% (6.3 km^2) decline in the area of suitable gibbon forest habitat within BNNR over a 17-year period (1991-2008). This equates to an annual rate of habitat loss of around 0.4%. I therefore simulated a scenario in which this observed rate of annual habitat loss was imposed for the duration of the simulation (through a change in K) to predict the likely outcome should this level of habitat loss be allowed to continue unchecked. Without substantial political will and effective patrolling, the rate of commercial and illegal logging, as well as the harvesting of non-forest timber products by local villagers presently occurring (pers. obs., June 2012), could easily increase. So, to investigate the consequences of a higher rate of habitat loss, I also simulated annual rates of loss of 1%, 2%, and 5%, again for the duration of the simulated time period.

Catastrophe

Catastrophes are remarkable events outside the bounds of normal environmental variation, e.g. natural disasters. Such events can impact the survival and/or reproduction of wild populations (Shaffer 1981). Within VORTEX catastrophic events are simulated by assigning a probability of occurrence and a severity factor ranging from 0.0 (maximum or absolute effect) to 1.0 (no effect). To explore the impact of a catastrophe, I developed two models capturing increasing levels of risk of occurrence and severity of impacts. The models represent both generic models of catastrophes of the specified frequency and magnitude, and likely catastrophes that may affect the population:

i) A moderate catastrophe (e.g. typhoon), with 5% risk of occurrence, and 10% reduction (severity factor 0.90) in both survival and reproduction.

ii) A severe catastrophe (e.g. disease), with 20% probability of occurrence, 50% reduction in survival (severity factor 0.50), and 20% reduction in reproduction (severity factor 0.80).

Moderate catastrophe: Typhoon

Typhoons, cyclonic storms with sustained winds of at least 33 ms^{-1}, are a regular occurrence in Hainan; typhoon season lasts from May-November, with peak frequency in September (Wang et al. 2012). Typhoons can cause extensive damage and loss of life; for example, in 2003, Typhoon Nepartak caused damage in Hainan estimated to be RMB 1.63 billion Chinese Yuan (c. USD 200 million), including loss of crops and livestock (People's Daily 2003) , and recent 'super' Typhoon Haiyan killed thousands of people in the Philippines (BBC 2013) and seven in Hainan (New Straits Times 2013). Climate change predictions indicate that typhoon frequency and severity is likely to increase (Mann and Emanuel 2006, Knutson et al. 2010), and there is a substantial risk a typhoon of substantial intensity could traverse directly through Bawangling.

There are no available data on the effect of typhoons on gibbon populations, but the predominant effect will likely be destruction and disturbance of the forest integrity (fallen trees, disconnected canopy etc.). Significant declines in canopy cover have been detected following typhoons in Taiwanese forests (Lin et al. 2003). A high-intensity typhoon could also result in gibbon deaths, both as a result of the immediate impact of the storm, and a reduction in forest quality (e.g. fruit load) leading to increased mortality. Indeed, hurricane damage has been shown to impact frugivorous forest birds most severely (Lynch 1991). Evidence indicates that the Hainan gibbon breeding cycle may be tied to peaks in food availability (Zhou et al. 2008b), so the breeding capacity of the population may be sensitive to changes in fruit and flower loads, and reduced food abundance following a typhoon may also reduce reproduction in surviving individuals. Therefore, to investigate the impact of such a catastrophe on the Hainan gibbon population, I modelled a scenario in which both survival and reproduction were reduced, with severity values set arbitrarily in the absence of data supporting specific figures.

Available data on the occurrence of typhoons in the Western Pacific region indicate an annual average of 1.66 cyclones per year, or 166 cyclones in 100 years making landfall in Hainan (calculated from count data for 1945-2007 presented in Wang et al. 2012) . It is not clear how many of these typhoons track through Bawangling each year, or the proportion that are of sufficient intensity to substantially compromise habitat structure and vertebrate life within the reserve. However, if we assume a moderate 5% risk of occurrence of this type of catastrophe befalling the population (i.e. 5 typhoons in every 100 years), this equates to 3% of the 166 typhoons that land in Hainan in 100 years tracking directly through BNNR at a sustained intensity sufficient to cause significant damage to the gibbon population, which is likely a reasonably conservative estimate.

Severe catastrophe: Disease

Small populations may be particularly vulnerable to disease as a result of reduced genetic diversity conferring reduced natural resistance within the population. Given the reduced genetic diversity within the Hainan gibbon population (see Chapter 4), a disease epidemic could be catastrophic for the species, and such a catastrophe presents a real risk to the species' survival. The taxonomic and physical proximity of the Hainan gibbon population to humans, with the fragmented condition of BNNR and at least one social group (Group C) ranging near to neighbouring villages (see Chapter 3), may make the population susceptible to zoonotic disease transmission, as observed in wild populations of other apes (Wolfe et al. 1998, Wallis and Lee 1999). Human diseases may lead to mortality in gibbons, with at least one documented incidence of the death of a captive white-handed gibbon (*Hylobates lar*) due to human herpesvirus type 1 (HHV-1) (Landolfi et al. 2005). Furthermore, rhesus macaques (*Macaca mulatta*) have been observed to feed on individual fruiting trees at the same time as Hainan gibbons (Chan et al. 2005), which has implications for inter-species disease transmission (Pedersen and Davies 2009).

Again, there is no available information on the probable impact of diseases in wild gibbon populations. Few exact data on such impacts exist for wild populations of other non-human hominoids. However, there is evidence that an Ebola outbreak caused an 80% decline in gorilla (*Gorilla gorilla*) and chimpanzee (*Pan troglodytes*) populations in the Gabon/Republic of Congo border region between 2001-2003 (Walsh et al. 2003). Furthermore, a new species-specific strain of pneumonia caused an 31% decline in survival in the chimpanzee population in Taï National Park, Côte d'Ivoire, in just one week (Leendertz et al. 2006, Boesch 2008). Given the gregarious nature of gibbons, it is therefore not unreasonable to assume that an outbreak of a particularly virulent disease could kill half of the remaining Hainan gibbon population in one instance. I also incorporated an impact to reproduction, as disease can reduce mammal fecundity in surviving individuals (Feore et al. 1997, Graham et al. 2010), although impacts on primate reproduction in wild populations are not well documented. Quantitative data on the probability of disease occurrence within wild primate populations are also scarce, but ongoing observation of the Taï National Park chimpanzee population recorded four distinct disease outbreaks (different pathogens) causing severe mortality in the population (12-31%) over a 12 year period (Boesch 2008), equating to a 30% risk of occurrence. There is also evidence to suggest that most vertebrates are at risk of catastrophic die-off, i.e. 50% of the population or more within one year, at a rate of 14% per generation (Reed et al. 2003), indicating much lower risk. Consequently, the employed probability of occurrence, one outbreak every five years (20%), may be a generous estimate of the risk of a severe catastrophic impact, but is in keeping with limited available primate-specific data from the wild.

Complex threat models

A small population may be relatively resilient to individual extrinsic threats and catastrophes if they are of a moderate nature and experienced in isolation. However, in reality, it is rare for a population of an endangered species to experience only one threatening process, with a complex combination of threats being the cause of many threatened species' declines. The Hainan gibbon was driven to its tiny population size through a combination of targeted hunting and ongoing habitat clearance. It is therefore vital to investigate the viability of the population when impacted by multiple threats and catastrophes simultaneously. I modelled two scenarios in which the likely threats and risks of catastrophe were combined within a simulation. The two scenarios represented situations that were increasingly severe and under which we would expect reduced viability:

a) A moderate threat of hunting (1 pair every ten years), habitat loss at the reported rate for the BNNR region (-0.4% annually, constant), and a catastrophe of moderate nature, as per the typhoon scenario (5% risk, severity factors 0.90 for both survival and reproduction).

b) As above but with the catastrophe being of severe nature, as per the disease scenario (10% risk, severity factors 0.75 for survival and 0.80 for reproduction).

Conservation management actions

In addition to the principal aim of investigating the likely outcome of taking no conservation action, the second aim of this PVA was to investigate the probable outcome of a subset of possible management actions that could potentially be implemented in an attempt to conserve the population. There are often high risks associated with intensive management actions, while other actions may be less risky but can require significant investment and take longer to produce tangible outcomes. So, in a climate of limited conservation funds, it is beneficial to be able to predict the outcome of potential management actions so that they may be evaluated within the context of evidence for or against their implementation (evidence-based conservation planning). This is especially important for the Hainan gibbon, for which only one population persists within one forest fragment, meaning the stakes are high and the opportunities for success are finite.

I investigated two potential management actions in separate model simulations in order to improve our understanding of their possible outcomes. These models signify simplified representations of the possible actions examined within the limitations of the VORTEX framework, and the constraints of available information. The management actions explored here by no means constitute the full suite of those available, but represent obvious potential actions that were possible to model in the VORTEX setting. To determine under which conditions (if any) these management actions may alter the fate of the population, I simulated multiple scenarios for each action in which the number of threats incorporated and the level of catastrophic risk and severity were varied to simulate increasingly complex and adverse situations. I did not generate permutations under the simple baseline model settings (no threats), as this likely represents an overoptimistic view of the population's situation. Model outputs were compared to the status quo catastrophe and complex threat combination models to assess the extent of improvement in viability, or otherwise, we might expect under each management action.

1. Increased available habitat

Limited available habitat is one of the factors proposed as responsible for the limited growth of the Hainan gibbon population (Chan et al. 2005). Regardless of which estimate of the species' home range requirements we accept (see Chapter 3), the current 15 km^2 of suitable habitat within BNNR is a tiny forest fragment and will permit only a finite amount of population growth. Therefore, an obvious potential management action is to increase the habitat available to the population. In fact, in 2005 around 16,000 seedlings of 30 gibbon food tree species were planted within a degraded section of BNNR in an attempt to increase the available habitat (Chan et al. 2005), and the BNNR Management Office is eager to conduct additional reforestation within the reserve (BNNR Management Office pers. comm., July 2011). This management option is particularly appealing as it is a relatively low-risk, non-invasive strategy, meaning that there is a possibility that involved parties will see reforestation as the simplest management solution for the population. However, the time required for seedlings to mature may be too long to provide any meaningful benefit to the population and, as yet, we have no quantitative information regarding exactly what degree of influence this action may have upon the population, including any improvement that could be seen in population viability.

To investigate this question, I modelled a scenario in which the suitable habitat available to the Hainan gibbon population was doubled, i.e. an additional, contiguous forest fragment equal in size to that presently existing (15 km^2) became available to the current population. Such an increase would represent substantial habitat expansion, but the model was designed to determine whether any improvement in viability could be achieved under at least this level of management. To explore this potential management action in detail, I modelled two scenarios to represent the two principal ways in which this habitat increase may be achieved:

i) The additional habitat was immediately available to the population, i.e. *K* increased by 100% in the first year, to mimic what would happen if it was possible to increase the suitable habitat without any delay. This could be achieved by connecting existing small, fragmented patches of suitable habitat within/outside BNNR. Gibbons will not cross large gaps (>10 m) in the canopy (Das et al. 2009a), therefore aerial connections will be required to achieve this. *Hoolock* gibbons have been observed to utilise canopy bridges, brachiating efficiently across bamboo poles, indicating these are a viable tool for re-establishing connectivity of fragmented gibbon habitat (Das et al. 2009b). Therefore, this scenario assumed such tools were used to connect adequate suitable habitat already existing in and near to the reserve to achieve the immediate 100% increase.

ii) The habitat only began to become available after a period of around 30 years, with a gradual increase to the full 100% expansion of habitat over a subsequent 30 year period. This scenario was designed to represent the likely situation in which there is a time lag before the planted forest matures to a point at which it will become suitable structurally and in terms of food productivity to gibbons (i.e. ≥20 cm diameter at breast height; Hamard et al. 2010). Published data enabling estimation of likely rates of recovery for Hainanese forests are generally unavailable, but existing data for other tropical forests indicate forest structure, density, basal area, biomass, and species richness in restored secondary forests can approach that of old growth (>80 years) forest sites after approximately 40 years (Saldarriaga et al. 1988, Aide et al. 2000, Guariguata and Ostertag 2001). Similarly, information on when gibbons will begin to use restored forest patches is also uncommon, but at least one study found gibbon densities were more than double in forest patches 30 years post-logging compared to patches with only 15 years recovery time (Phoonjampa et al. 2011). Therefore, a lag of 30 years, then continued increase in forest availability coinciding with forest maturation (up to 60 years), was used as a reasonable estimate.

In both increased habitat scenarios I made the simplifying assumptions that only one such increase was achieved, and that no habitat loss occurred simultaneous to the increase in available habitat. The results of these models are therefore contingent upon habitat loss being controlled. I did, however, incorporate the threats of catastrophe (moderate and severe) and hunting (one pair every 10 years) in four models simulating different combinations of these factors.

2. Translocation

With just one Hainan gibbon population persisting in one forest fragment within one nature reserve, an obvious risk-management strategy could be to translocate a subset of the population to a separate tract of protected forest to establish a second population. ‘Translocation’, or the deliberate movement of wild animals from one natural habitat to another, is often conducted for the purpose of conservation or management (IUCN-SSC 2013), and is distinguished from ‘reintroduction’ where captive animals, usually captive-bred or rescued/rehabilitated individuals, are transferred into a wild area which was once part of their historical range (Beck et al. 2007). Despite their intended benefits, ‘conservation translocations’ present significant risks, including: possible death of animals as a result of husbandry issues during capture, transport and time in captivity (Armstrong et al. 1999); death in-situ after translocation due to insufficiently controlled threats (e.g. predators) (Griffin et al. 2000); and dispersal of translocated individuals away from the site back to the source location (Groombridge et al. 2004). More fundamental in cases where the remaining population is exceptionally small, is the risk to the source population. The IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN-SSC 2013, pp. 8-16) state that “except under rare circumstances, removing individuals for translocation should not endanger the source population” and “where risk is high and/or uncertainty remains about risks and their impacts, a translocation should not proceed”. Therefore, it is important to investigate the potential impact of a translocation programme.

No formal guidelines for gibbon translocation exist to inform the model in terms of what a sustainable size and periodicity of animal transfer may be (although it is within the mandate of the newly-formed IUCN SSC PSG Section on Small Apes to canvas the issue of gibbon translocation). Few wild-to-wild gibbon translocations have been documented (but see report by The Times of India 2012). While there have been some efforts to try to determine general rules for optimal translocation strategies (Lubow 1996, Rout et al. 2007), it is apparent that there is no one-size-fits-all approach (Tenhumberg et al. 2004). So, despite a wealth of literature on different translocation efforts with different goals, the inherent complexity and situational-specificity of this action means that it is difficult to draw any conclusions from previous translocation programmes about how to ensure a ‘successful’ and sustainable conservation translocation regime.

I therefore developed a simplified model of translocation, in which a small subset of the population, one existing social group (Group C, 3 individuals), was translocated in a single event to a new (geographically separate) location with an area equivalent to the size of the available habitat in BNNR (15 km^2), creating two subpopulations with no dispersal between them. This simple model was designed to focus on the impact which translocation, even just a single event, may have upon the source population to determine if such an action may compromise the population, and is therefore only intended as a first step in assessing the risks of this action. For simplicity, and in the absence of specific potential site locality information, I allowed for the survival of all individuals during translocation (capture, ex-situ holding and release), assumed that the new location had similar quality habitat and thus the same carrying capacity, and the population had the same demographic rates as the current population. The model started after the translocation event, and relatedness within (and between) the populations was incorporated using a pedigree to specify the two starting populations.

To explore the relative performance of translocation in different situations, for the source population I incorporated the risk of catastrophe (moderate and severe) and threats of hunting (one pair every 10 years) and habitat loss (-0.4% annually) in eight models simulating the different combinations of these factors. I assumed that new location, and hence the translocated population, would also be subject to catastrophes and suffer the same catastrophe risks and impacts as the current population, given the manner in which these catastrophe parameters were derived. However, I did not impose any additional threats upon the new population, as given the costs and risks associated with such a measure, it is reasonable to assume that extensive pre-screening of proposed destinations would be conducted to ensure these threats were removed before translocation, as per international guidelines (IUCN-SSC 2013). The input parameters used in the translocation models are summarised in Table 6.2. The viability of the source and translocated populations, and that of the species or ‘metapopulation’ (source and translocated populations together), were assessed.

Measures of viability

Many conservation-orientated PVAs report the probability of extinction predicted under a given scenario, but there are several quantitative measures which can be used to evaluate population viability under different model contexts (Akçakaya and Sjogren-Gulve 2000). There is no consensus on which viability measure is most suitable (e.g. see Pe'er et al. 2013), and different measures reveal different aspects of the population’s (projected) behaviour and so can answer different questions. Furthermore, given the inherent limitations of PVA, which like all population modelling will only be as accurate as the input data, it is advisable to assess multiple measures of viability under each scenario and compare these measures across scenarios, rather than assuming the models point solely to absolute probabilities of reaching extinction (Akçakaya and Sjogren-Gulve 2000, Reed et al. 2002). Therefore, I report the following measures of viability, all generated over the simulated time period of 150 years:

- **Stochastic growth rate (r_s)** observed growth rate taking into account stochastic processes (c.f. deterministic r which does not), prior to any truncation in population size exceeding K (as this more accurately represents the growth potential of the population), with standard deviation across iterations (**SD (r_s)**)

- **Probability of extinction (PE)** of the population – proportion of iterations (in 1000) that went extinct
- **Mean Time to Extinction (TE)** – for those iterations that suffer extinctions, in years
- **Mean final population size, extant populations (N-extant)** – mean population size in final year of simulation from those populations that did not go extinct
- **Mean final population size, all populations** (**N-all**) – mean population size in final year of simulation from all populations
- **Gene Diversity (GD)** – mean expected heterozygosity remaining in extant populations in final year of simulation, expressed as a percentage of initial population's gene diversity

Results of scenarios were compared to assess relative population persistence under different threat and management situations, rather than defining the population as 'viable' or otherwise by setting thresholds of these viability measures. This approach will also permit interpretation by other stakeholders with different ideas about acceptable levels of risk/growth when assessing population viability under a particular scenario.

Table 6.2 Parameter values used in VORTEX PVA models to investigate translocation as a potential conservation management action. For the source population: models were run with risk of moderate/severe catastrophe only; with catastrophe risk plus threat of hunting or habitat loss; and with catastrophe risk plus threats of both hunting and habitat loss. For translocated population: models were run with risk of moderate/severe catastrophe only. Source and translocated populations were subject to corresponding catastrophe risk (moderate/severe) within a given scenario.

Input parameter	**Population 1 (source)**	**Population 2 (translocated)**
No. of populations	1	1
Initial population size	**22**	**3**
Genetic management	Initial population pedigree	Initial population pedigree
No. of iterations	1000	1000
No. of years	150	150
Extinction definition	Only 1 sex remains	Only 1 sex remains
Stable age distribution	No, specified by pedigree	No, specified by pedigree
Inbreeding depression	Yes	Yes
Lethal equivalents	6	6
Reproductive system	Long-term polygyny	Long-term polygyny
Age of first offspring for females	8	8
Age of first offspring for males	10	10
Maximum age of reproduction	30	30
Maximum no. of broods/year	1	1
Maximum no. of progeny/brood	1	1
Sex ratio at birth (% males)	50 (75)	50 (75)
Adult females breeding (%)	(2 year IBI) 50	(2 year IBI) 50
EV in % females breeding	5 (=10%)	5 (=10%)
Mortality (%) age 0 to 1 (infant)	10 (SD=2)	10 (SD=2)
Mortality (%) age 7 to 8 (dispersal)	25 (SD=5)	25 (SD=5)
Mortality (%) all other age classes	5 (SD=1)	5 (SD=1)
Males in breeding pool (%)	100	100
Carrying capacity ('*K*')	30	30
Change in *K* (Habitat loss)	none; -0.4% (annual rate over 100 years)	none
Harvest (Hunting)	none; 1 pair (1 male and 1 female) every 10 years	none
No./type of catastrophes	Moderate (typhoon); Severe (disease)	Moderate (typhoon); Severe (disease)
Catastrophe frequency	5% (moderate); 20 % (severe)	5% (moderate); 20 % (severe)
Catastrophe severity factors (Reproduction, Survival)	0.90, 0.90 (moderate); 0.80, 0.50 (severe)	0.90, 0.90 (moderate); 0.80, 0.50 (severe)

Results

Baseline model

The baseline model described a population with positive deterministic growth rate, intrinsic rate of increase r= 0.034 and finite growth rate of λ = 1.034, indicating an annual growth rate of around 3.4% per year. This is the average growth that could be expected in the absence of stochastic processes, inbreeding, and extrinsic threats, based upon the specified rates of fecundity and mortality, and therefore indicates the growth potential of the population under 'ideal' conditions. This deterministic annual growth rate is roughly in line with that observed for *Nomascus nasutus* (3.7%; Fan Peng Fei pers. comm., August 2013), the most closely related species, and both are slightly higher than other gibbon species with annual deterministic growth rates of between 1.2% and 2.6% reported for *Hylobates*, *Hoolock* and *Nomascus* species (Supriatna et al. 1994, Tunhikorn et al. 1994, Molur et al. 2005, Traeholt et al. 2005). This is likely a result of a combination of the interbirth interval (IBI) and mating system observed for the Hainan gibbon, as well as the increased dispersal mortality. An IBI of 2 years (50% of females breeding) would permit a faster rate of population growth compared to a 3 year IBI (33% of females breeding), as observed for other gibbon species. Additionally, long-term polygyny will further increase the population growth rate, as indicated by the higher rates observed for both the Hainan gibbon and *N. nasutus*, both reported to display this mating system. The apparent elevated mortality at the age of dispersal would then lower the rate slightly. The observed deterministic growth rate is therefore feasible for this long-lived mammalian species with an apparently elevated capacity for reproduction.

The baseline model revealed that even in the absence of external threats and catastrophes the viability of the Hainan gibbon population is compromised. The growth potential of the population taking into account stochastic pressures was predicted to be very low (r_s= 0.004), with the population forecast to remain very small as a result, likely to fall to a final population size of around 17 individuals in the next 150 years. The probability that the population would become extinct in this time was 31.2% in a mean time of 115.6 years, and 63% of the current gene diversity was projected to remain if the population survives. This represents the absolute best-case scenario if the population is left at status quo.

Demographic sensitivity testing

The baseline model showed uncertainty in model projections as a result of uncertainty in a number of key demographic input variables, with the greatest sensitivity due to uncertainty in sex ratio of offspring. When the ratio of male offspring born was 75%, the stochastic growth potential of the population fell (r_s= -0.015) (Figure 6.2) and probability of extinction was predicted to be as high as 98.4% (Figure 6.3), with the population likely to decline to seven individuals within 150 years, and gene diversity predicted to fall to 43% of the initial population (Figure 6.4). This demographic variable produced the greatest variation in the three viability measures assessed over the smallest relative input range (50%-75% male, relative change +50%), indicating greatest model sensitivity to this demographic variable. Due to general concerns about the sex ratio of offspring in the current population, I used a balanced offspring sex ratio as default but also ran additional runs of each threat and management model specifying a male-biased ratio (75% males) to determine population viability under this added constraint. This allowed for uncertainty in this key parameter and investigation of how a biased sex ratio might alter the probable fate of the population within each scenario.

Varying the level of mortality at age of dispersal produced the largest overall variation in stochastic growth rate and probability of extinction (Figures 6.2, 6.3), and substantial variation in gene diversity (Figure 6.4). Relative to the range of input values tested, less variation in viability was observed by altering dispersal mortality more extensively (-60% to +100%) than that produced by altering the sex ratio at birth. Projections indicated that if dispersal mortality could be reduced to 15%, then the viability of the population would improve (r_s=0.014), gene diversity would increase (GD=0.66), and probability of extinction would decrease to c. 11%. However, if we have underestimated dispersal mortality and this is actually as high as 50%, then the outlook for the population, even in the absence of any threats or catastrophes, is predicted to be dire, with a probability of extinction >95% and final population size of surviving populations <10 individuals. It is apparent that under a condition of 30% dispersal mortality, r_s would become essentially zero (Figure 6.2). The actual population has experienced a small amount of growth in recent years (to presently observed 25 individuals) so it appears the baseline value of 25% mortality at dispersal age, which allows for minimal growth (very slightly positive r_s=0.004), is appropriate.

The baseline model also showed marked sensitivity to variation in other demographic variables which can be largely ignored. Altering the percentage of females breeding to 33%, as reported for other gibbon species, predicted lower population viability (r_s= -0.017, PE=88%, GD=0.53), as expected. This is important to note for future reference, should any conflicting information concerning the species' IBI become available. However, as all existing observations support an IBI of 2 years, we can essentially disregard uncertainty in this variable and use the results of the baseline model. Similarly, while the number of lethal equivalents specified greatly altered stochastic growth rate and probability of extinction, the most extreme values (r_s= -0.009, PE= 82.2%) were only observed when the number of lethal equivalents was doubled (to 12; relative change +100%). Relative to the sensitivity observed for the above demographic variables, this is less severe, so the baseline value can be assumed to adequately represent this factor.

In addition to the influence of the level of dispersal mortality, sensitivity testing indicated a second variable that should be considered for conservation management of the population. Increasing carrying capacity in the baseline model positively influenced population viability predictions. An increase of just 60% (*K*=50) allowed a higher stochastic growth rate (r_s=0.015), reduced probability of extinction to 4.3%, and improved gene diversity (remained at 75% of initial population). This *K* also allowed the population to grow above the apparent current limit (25 gibbons) to almost 38 individuals (N-extant=37.97). This result verified that the baseline setting was appropriate (allowing for only minimal growth as observed for the population) and that exploring an increase to available habitat as a management option was advisable. All other demographic variables produced comparatively small and largely negligible sensitivity in viability, indicating the employed baseline values were likely an appropriate approximation of the species' demography.

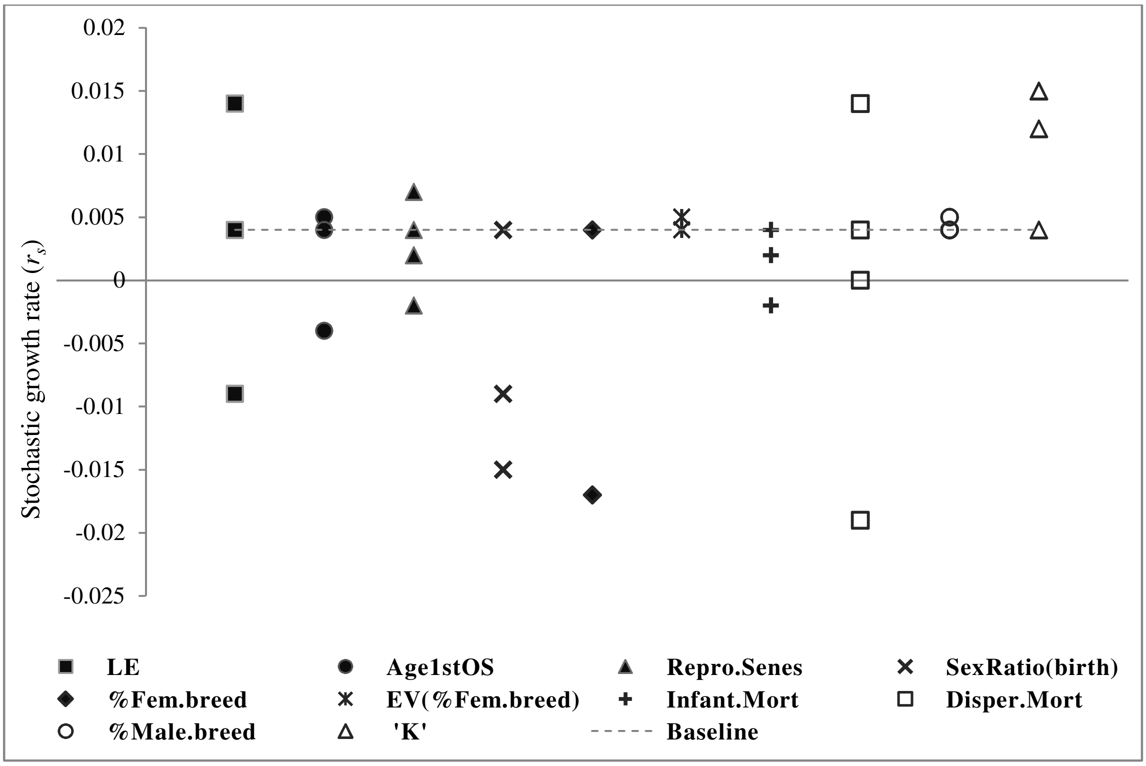


Figure 6.2 Sensitivity analysis of stochastic growth rate (r_s) for baseline model, showing rate variation (projection sensitivity) for each demographic parameter over range of values tested (represented as different symbols). Dashed line represents r_s for baseline model (baseline demographic variable values).

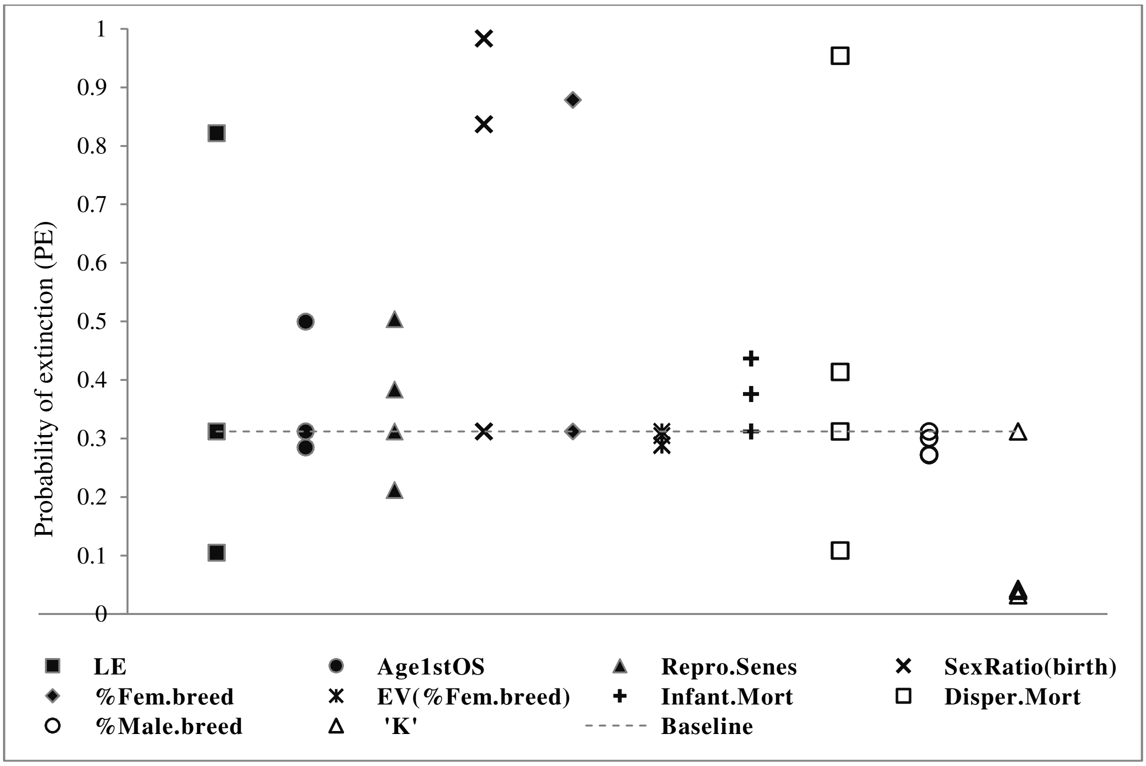


Figure 6.3 Sensitivity analysis of probability of extinction (PE) for baseline model, showing variation in probability (projection sensitivity) for each demographic parameter over range of values tested (represented as different symbols). Dashed line represents PE for baseline model (baseline demographic variable values).

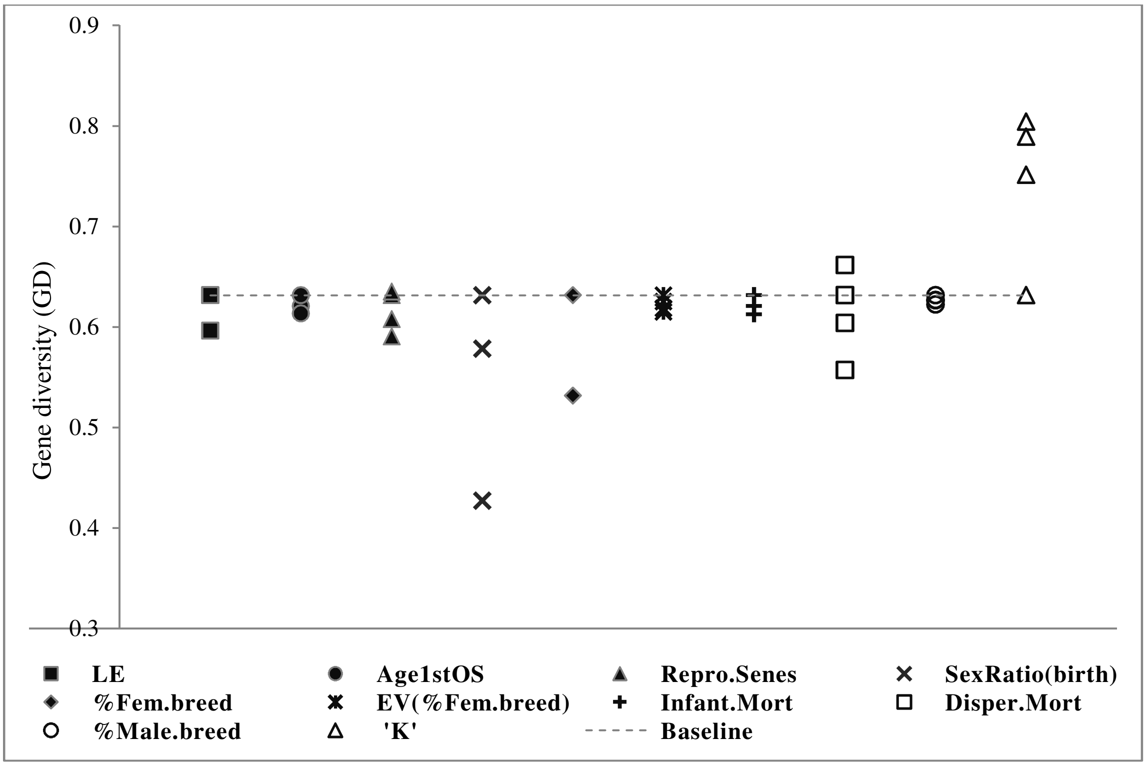


Figure 6.4 Sensitivity analysis of final gene diversity (GD) for baseline model, showing variation in remaining diversity (projection sensitivity) for each demographic parameter over range of values tested (represented as different symbols). Dashed line represents GD for baseline model (baseline demographic variable values).

Threat models

Hunting

When the lowest level threat of hunting was incorporated, probability of extinction increased to 82%, in a mean time to extinction of 100.6 years. Should the population survive, population size is predicted to fall to 13 individuals and gene diversity to 61% of the starting population (Table 6.3). If the risk of hunting exceeds this level (5%/individual/year), population viability is predicted to fall drastically. Probability of extinction increased to virtually 100% under all three higher hunting levels, and time to extinction ranged from 73.4 years (with removal of 1 pair/5 years) to as little as 12.4 years if the removal rate reaches 1 pair/year. The latter level may be unrealistically high, but serves to demonstrate the major influence this threat has upon population viability. The stepwise increase in vulnerability to increasing hunting threat is also clear from the predicted trajectory of mean population size (N-All) over the next 150 years at different hunting levels (Figure 6.5). If the existing population's sex ratio of offspring is 75% male (rather than equal), then even the lowest level of hunting will greatly compromise the fate of the population, predicted to result in extinction (PE=100%) in less than 48 years. Clearly, if the risk of hunting cannot be removed, the species' risk of extinction will be extreme, even in the absence of other threats.

Habitat loss

Taking into account the current observed rate of habitat loss for BNNR roughly doubled the baseline probability of extinction, although mean time to extinction remained close to 115 years (PE=61%, TE=114.1, Table 6.3). Genetic diversity was predicted to be greatly impacted by this rate of habitat loss (GD=0.49), indicating that while the threat of hunting may more severely increase the chance of extinction, habitat loss will greatly compromise the genetic resilience of the population. If the rate of habitat loss observed by Zhang et al. (2010) increases, then the population will be at great risk of extinction. The effect of a slightly higher rate (1% annual loss) was extreme, predicted to result in population extinction (PE=100%) within less than 84 years. Still higher rates reduced mean time to extinction (PE=100%) to 45.7 years (2% annual loss) and 19.6 years (5% annual loss), indicating further habitat loss within BNNR will have a severe impact upon the population (evidenced by sharp declines to zero under these rates; Figure 6.6). Again, if the offspring sex ratio is male biased (75%), then habitat loss simply at the recently observed rate will likely result in extinction of the species within less than 70 years (PE=99%, TE=68.9).

Table 6.3 VORTEX PVA model results for effect of threats (hunting and habitat loss) and catastrophe (moderate/severe) on population viability. Viability measures are: stochastic growth rate (r_s) and standard deviation (SD (r_s)); probability of extinction (PE); mean final population size, extant populations only (N-extant); mean final population size, all populations (N-all); mean final gene diversity (percentage of initial gene diversity remaining), extant populations only (GD); and mean time to extinction (TE), in years. Grey shaded cells indicate scenarios in which 100% of simulated populations went extinct.

Model	**Hunting level**	**Habitat loss level**	**Catastrophe type**	**Sex Ratio at birth (%males)**	r_s	**SD (r_s)**	**PE**	**N-extant**	**N-all**	**GD**	**TE**
BASELINE	**none**	**none**	**none**	**50**	**0.004**	**0.088**	**0.31**	**17.27**	**12.06**	**0.63**	**115.6**
Hunting	1 pair/10 years	none	none	50	-0.007	0.103	0.82	13.37	2.48	0.61	100.6
	1 pair/5 years	none	none	50	-0.020	0.114	0.99	8.00	0.12	0.54	73.4
	1 pair/2 years	none	none	50	-0.071	0.138	1	-	-	-	27.0
	1 pair/year	none	none	50	-0.172	0.162	1	-	-	-	12.4
	1 pair/10 years	*none*	*none*	*75*	-0.021	0.102	1	-	-	-	47.7
Habitat loss	none	-0.4% annually	none	50	0.001	0.102	0.61	7.07	3.00	0.49	114.1
	none	-1% annually	none	50	0.005	0.110	1	-	-	-	83.5
	none	-2% annually	none	50	0.010	0.110	1	-	-	-	45.7
	none	-5% annually	none	50	0.018	0.107	1	-	-	-	19.6
	none	*-0.4% annually*	*none*	*75*	-0.014	0.101	0.99	6.75	0.08	0.38	68.9
Catastrophe	none	none	Moderate (typhoon)	50	-0.001	0.098	0.46	14.54	8.07	0.59	110.1
	none	none	Severe (disease)	50	-0.099	0.302	1	-	-	-	19.2
	none	*none*	*Moderate (typhoon)*	*75*	-0.018	0.106	0.99	4.83	0.04	0.43	67.3
	none	*none*	*Severe (disease)*	*75*	-0.099	0.298	1	-	-	-	17.6
Complex threat combinations	1 pair/10 years	-0.4% annually	Moderate (typhoon)	50	-0.015	0.118	0.99	5.17	0.04	0.51	82.3
	1 pair/10 years	-0.4% annually	Severe (disease)	50	-0.113	0.307	1	-	-	-	16.9
	1 pair/10 years	*-0.4% annually*	*Moderate (typhoon)*	*75*	-0.023	0.109	1	-	-	-	43.6
	1 pair/10 years	*-0.4% annually*	*Severe (disease)*	*75*	-0.111	0.299	1	-	-	-	15.3

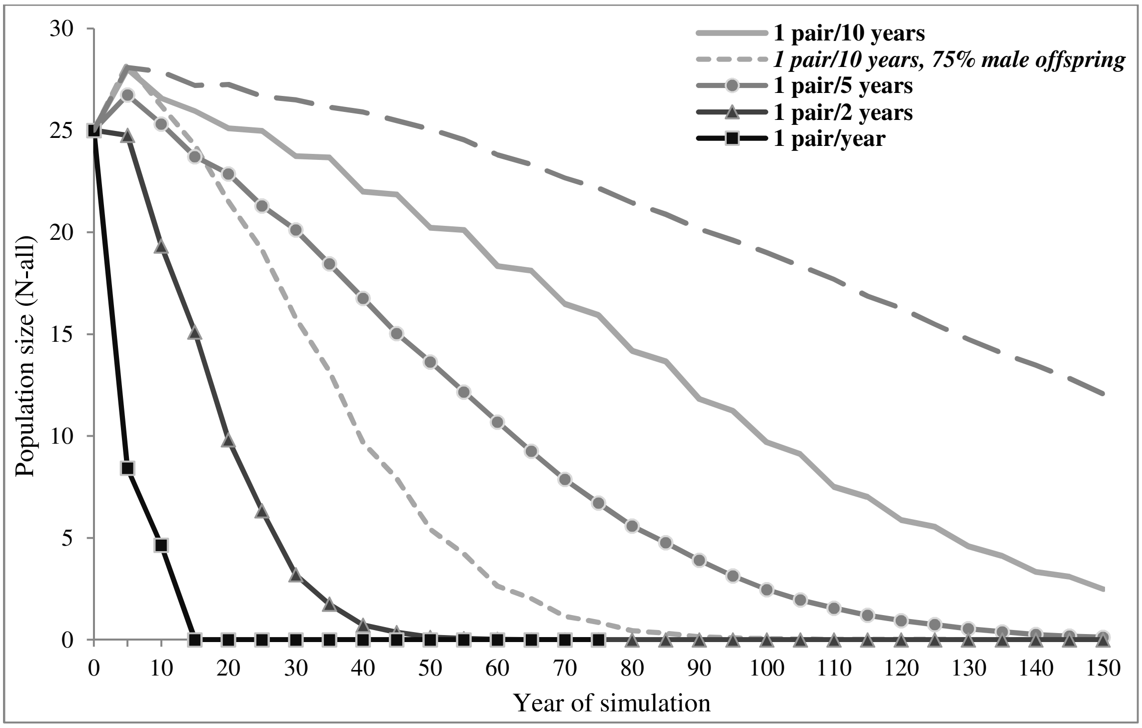


Figure 6.5 Projected mean final population size (N-all) over next 150 years under different hunting pressures (increasing intensity indicated by graduating darkness of lines). Lowest level but with condition of biased offspring sex ratio (75% male) indicated by small dashed line. Large dashed line represents baseline model (no threats/catastrophe). Where N-all becomes zero indicates population collapse in 100% of simulations (PE=100%).

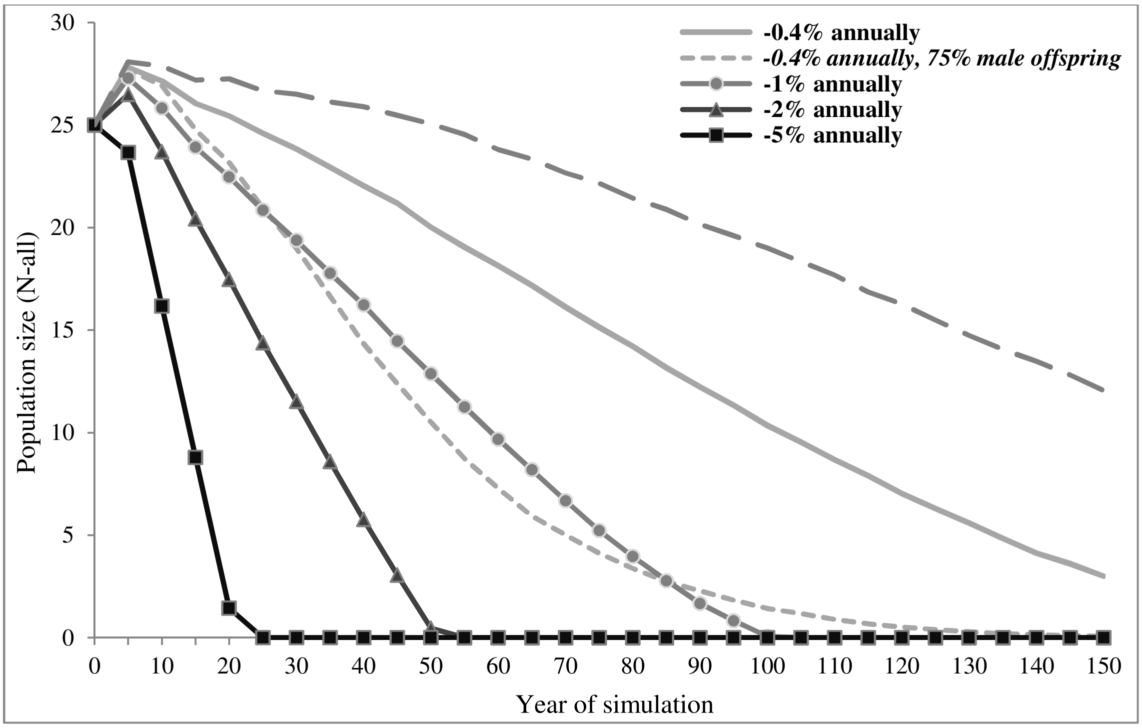


Figure 6.6 Projected mean final population size (N-all) over next 150 years under different levels of habitat loss (increasing intensity indicated by graduating darkness of lines). Lowest level but with condition of biased offspring sex ratio indicated by small dashed line. Large dashed line represents baseline model. Where N-all becomes zero indicates PE=100%.

Catastrophe

Including a catastrophic event of moderate severity increased probability of extinction to 46% with extinction likely to occur within 110 years. This level of catastrophe risk and impact also reduced predicted genetic diversity and population size, should the population survive (Table 6.3). A severe catastrophe would be disastrous for the Hainan gibbon population. Under such conditions the population is likely to become extinct (PE=100%) within less than 20 years. Again, when a bias in offspring sex ratio was included, population viability was further lowered under both catastrophe scenarios. Probability of extinction more than doubled for the moderate catastrophe model under this condition (PE=99%) and mean time to extinction almost halved (TE=67). For the severe catastrophe scenario, risk of extinction remained acute (PE=100%), and time to extinction shrank to 17.6 years. The extreme effect of a severe catastrophe, and even a moderate one if the population's offspring sex ratio is biased, is clear from the plot of projected mean population size of all simulated populations over the next 150 years (Figure 6.7).

Complex threat models

Incorporating the simultaneous negative impacts of hunting, habitat loss and a moderate catastrophe lowered the population's long-term viability more than each individual threat in isolation as expected, but the combined effect was acute. Probability of extinction increased to 99% with mean time to extinction 82.3 years (Table 6.3). Genetic diversity and final population size, should the population survive, are predicted to drastically decline (GD=0.51, N-extant =5.17). A male-biased offspring sex ratio compounded the situation further (Figure 6.8), reducing expected time to extinction to within 44 years. Allowing for a severe catastrophe unsurprisingly reduced viability even further, even with only modest levels of hunting and habitat loss. This combination of threats is highly likely to result in extinction in less than 17 years, slightly faster than under the risk of a severe catastrophe alone (Table 6.3, Figure 6.8). It is clear that a severe catastrophe would be devastating for the population, with or without the presence of other threats, with population collapse (PE=100%) predicted within 15-20 years in every scenario incorporating this level of catastrophe.

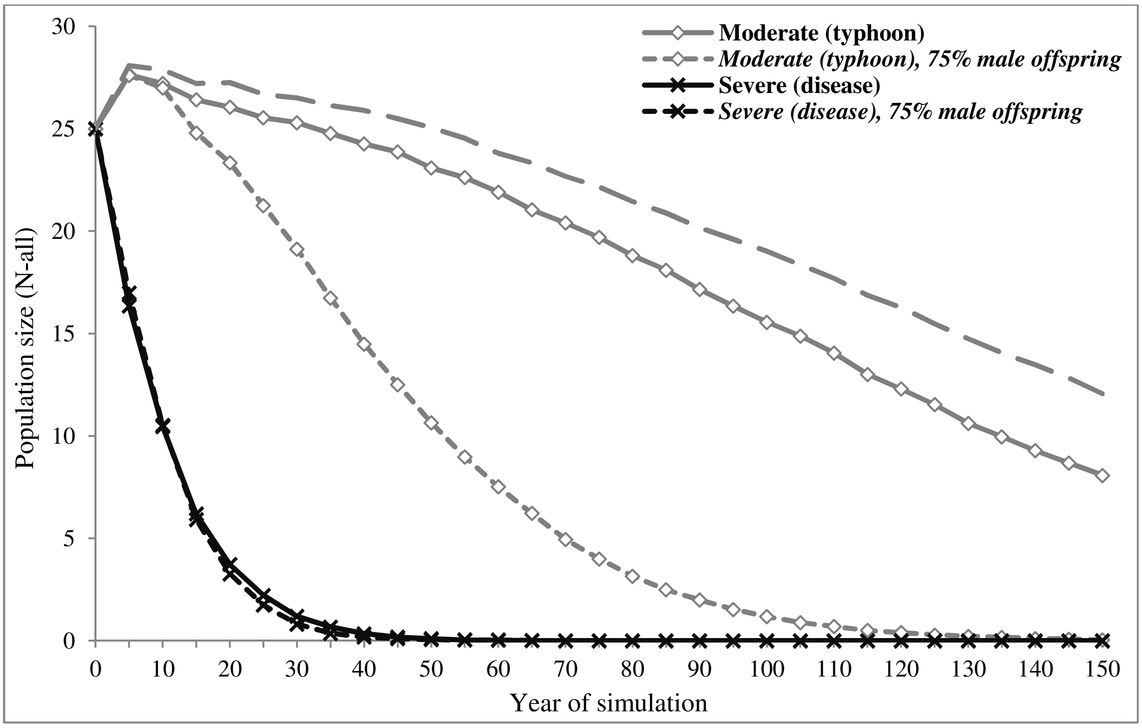


Figure 6.7 Projected mean final population size (N-all) over next 150 years under moderate (typhoon) and severe (disease) catastrophes (increasing risk and impacts indicated by graduating darkness of lines), and with condition of biased offspring sex ratio (75% male) as small dashed lines. Large dashed line represents baseline model (no threats/catastrophe). Where N-all becomes zero indicates PE=100%.

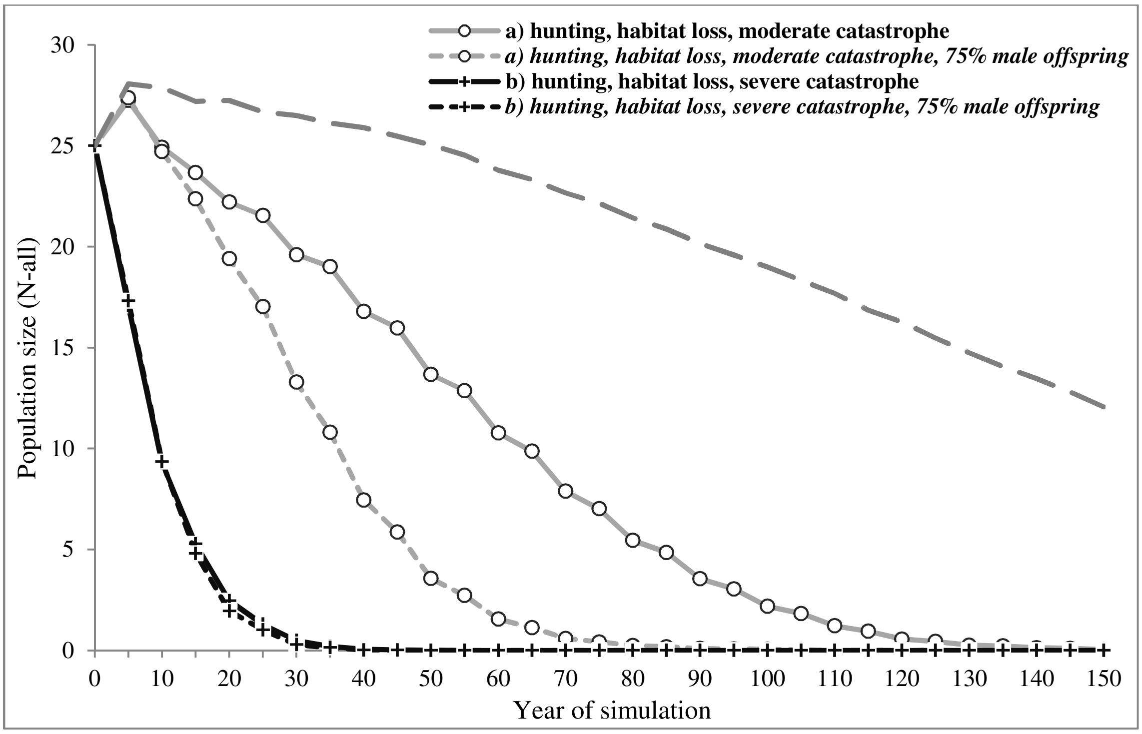


Figure 6.8 Projected mean final population size (N-all) over next 150 years under two complex threat combination models: a) hunting (1 pair/10 years), habitat loss (-0.4% annually), and moderate catastrophe (light lines); b) hunting, habitat loss, and severe catastrophe (dark lines). Dashed lines indicate projections with condition of biased offspring sex ratio. Large dashed line represents baseline model. Where N-all becomes zero indicates PE=100%.

Conservation Management Actions

1. Increased available habitat

Under the risk of only a moderate catastrophe, an immediate 100% increase in habitat improved population viability, with probability of extinction reduced from 46% to just 13% (Table 6.4, Figure 6.9). Immediately increasing the habitat also enhanced population resilience under the combined threats of hunting and moderate catastrophe, with probability of extinction more than halved from 99% down to 43%. Gene diversity also improved in both cases, being greater than that projected under each threat scenario and the baseline model (Table 6.3). Compared to the status quo model of the complex combination of threats, the increased habitat model assumes that habitat loss is controlled. Therefore, this improved viability is contingent on not just removal, but complete reversal of this threat. While making the additional habitat immediately available reduced the projected risk of population extinction under these threats, the time to extinction remained roughly the same with or without the increase (Figure 6.10). Furthermore, only modest population growth can be expected, with population size projected to reach less than 35 individuals in the presence of hunting and moderate catastrophe risks. If the threat of hunting can also be eliminated, population growth may improve slightly (N-extant=41.14).

Population viability also improved when a 30 year delay to habitat increase was incorporated, but again only in the scenarios assuming risk of a moderate catastrophe alone (PE= 0.31, GD=0.68), or combined risks of hunting and a moderate catastrophe (PE= 0.75, GD=0.69), although the degree of improvement was less than that under the immediate habitat increase (Table 6.4, Figure 6.9). Probability of extinction under moderate catastrophe was equivalent to that observed for the baseline model (assuming no threats or catastrophes; Table 6.3), indicating even a lagged habitat increase could enhance the population's resilience to a moderate catastrophe. Again, time to extinction remained close to equivalent status quo projections for each threat model (Figure 6.10), and final population size did not improve greatly, but was still larger than that predicted under such threats in the absence of habitat increase, delayed or otherwise (Table 6.3, 6.4).

Under a condition of 75% male bias in offspring, increasing available habitat immediately or allowing for a 30 year lag for forest maturation does not appear to improve population viability, with the population extremely likely to become extinct (PE≥98%), regardless of which and how many threats may be present (Figure 6.9). Increasing habitat immediately did, however, very modestly delay the time to extinction under this bias when catastrophic risk was moderate (Figure 6.10), indicating this may still be a worthwhile action under such circumstances. Unfortunately, increasing available habitat does not seem to insulate the population to the threat of a severe catastrophe. Probability of extinction remained at 100% for all scenarios in which this catastrophe was incorporated, and time to extinction ranged from 15-20 years (Table 6.4).

Table 6.4 VORTEX PVA model results for effect on population viability of increased available habitat as a potential management action, with 100% habitat increase: i) immediately; and ii) after 30 year lag. Viability measures as per Table 6.3. Grey shaded cells indicate scenarios in which 100% of simulated populations went extinct.

Model	**Hunting level**	**Habitat loss level**	**Catastrophe type**	**Sex Ratio at birth (%males)**	r_s	**SD (r_s)**	**PE**	**N-extant**	**N-all**	**GD**	**TE**
i) immediately	none	n/a	Moderate (typhoon)	50	0.007	0.074	0.125	41.14	36.04	0.75	102.7
	1 pair/10 years	n/a	Moderate (typhoon)	50	-0.002	0.087	0.431	34.55	19.70	0.75	89.5
	none	n/a	Severe (disease)	50	-0.099	0.300	1	-	-	-	20.0
	1 pair/10 years	n/a	Severe (disease)	50	-0.118	0.309	1	-	-	-	16.6
	none	*n/a*	*Moderate (typhoon)*	*75*	-0.020	0.101	0.98	7.00	0.23	0.61	75.6
	1 pair/10 years	*n/a*	*Moderate (typhoon)*	*75*	-0.026	0.103	1	-	-	-	50.9
	none	*n/a*	*Severe (disease)*	*75*	-0.100	0.295	1	-	-	-	17.7
	1 pair/10 years	*n/a*	*Severe (disease)*	*75*	-0.115	0.304	1	-	-	-	15.7
ii) after 30 year lag	none	n/a	Moderate (typhoon)	50	0.001	0.088	0.311	31.71	21.91	0.68	101.4
	1 pair/10 years	n/a	Moderate (typhoon)	50	-0.010	0.104	0.752	27.33	6.83	0.69	87.1
	none	n/a	Severe (disease)	50	-0.096	0.301	1	-	-	-	19.4
	1 pair/10 years	n/a	Severe (disease)	50	-0.118	0.309	1	-	-	-	16.4
	none	*n/a*	*Moderate (typhoon)*	*75*	-0.018	0.105	0.992	6.63	0.07	0.47	67.4
	1 pair/10 years	*n/a*	*Moderate (typhoon)*	*75*	-0.025	0.108	1	-	-	-	44.9
	none	*n/a*	*Severe (disease)*	*75*	-0.101	0.302	1	-	-	-	17.6
	1 pair/10 years	*n/a*	*Severe (disease)*	*75*	-0.114	0.305	1	-	-	-	15.3

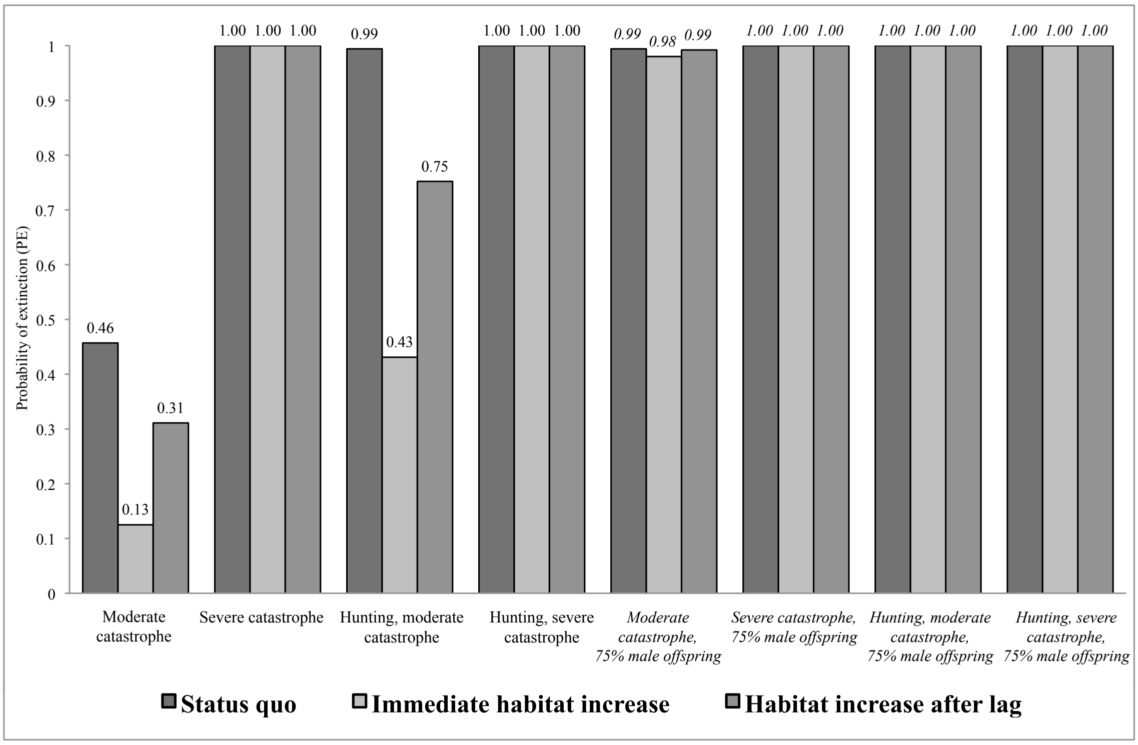


Figure 6.9 Projected probability of extinction (PE) under different possible management scenarios: left at status quo (with risk of threats and catastrophe and no conservation action); immediately increased available habitat; and after 30 year lag, with different threat/catastrophe combinations. Identical scenarios but allowing for biased offspring sex ratio (75% male) indicated by *italics*.

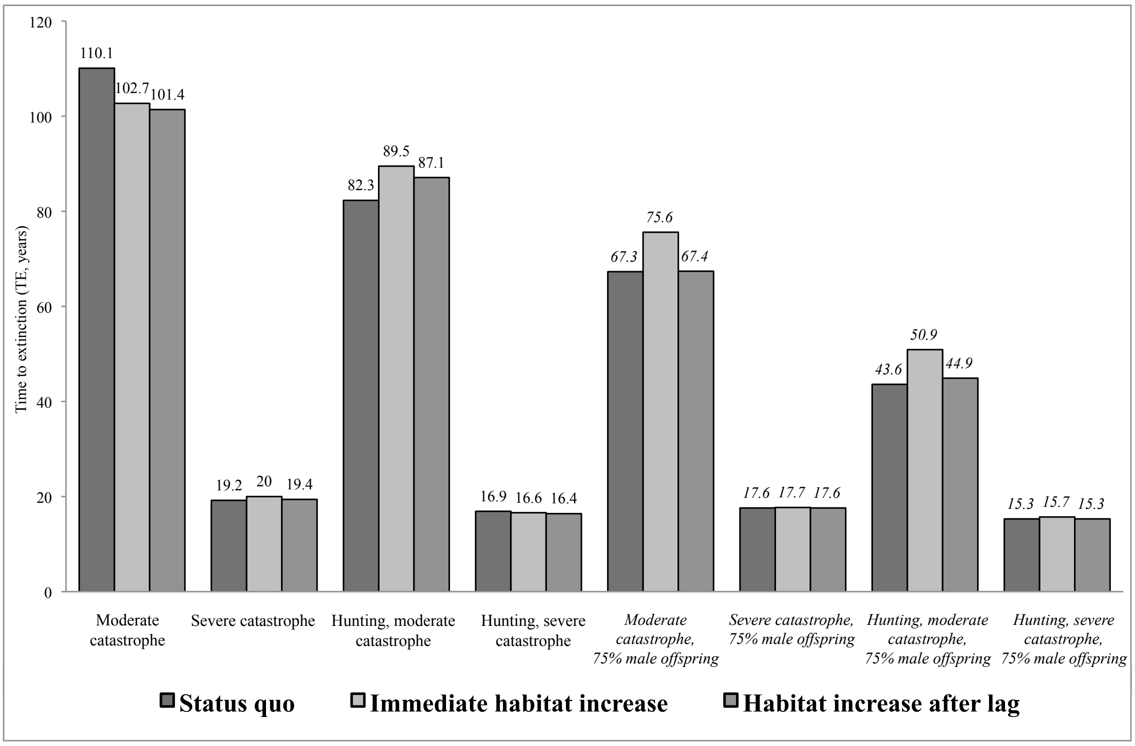


Figure 6.10 Projected mean time to extinction (TE, years) under possible management scenarios: left at status quo (with risk of threats and catastrophe and no conservation action); immediately increased available habitat; and after 30 year lag, with different threat/catastrophe combinations. Identical scenarios but allowing for biased offspring sex ratio (75% male) indicated by *italics*.

2. Translocation

With removal of just three individuals from the existing population, this simple translocation regime, rather than enhancing population viability, increased probability of extinction for the current (source) population by 19% compared to the likely outlook under the risk of a moderate catastrophe with no such conservation action (Table 6.5, Figure 6.11). Mean time to extinction also contracted very slightly, projected to occur six years earlier under the translocation model (Figure 6.12), but gene diversity remained the same (Table 6.3). These predictions also indicate that even if hunting and habitat loss could be eliminated, the removal of Group C could still compromise the current population. Incorporating the combined threats of hunting, habitat loss and moderate catastrophe, probability of extinction for the current population remained at 99% with the removal of Group C, mean time to extinction shortened by 7.1 years to 75.2 years, and gene diversity dropped by 12% to 0.39.

Under the more acute model combining hunting, habitat loss and severe catastrophe, the vulnerability of the source population remained as extreme following the removal of the subset of individuals (PE= 100%, TE= 15.2), as without their removal (PE= 100%, TE= 16.9). This was only slightly greater than the impact of a severe catastrophe alone upon population viability (PE=100%, TE=19.2), which would suggest that the danger of catastrophic disease probably presents a greater risk to long-term viability of the population than the removal of three individuals. Unfortunately, given the exceptionally high probabilities of extinction observed for all models incorporating severe catastrophe (Table 6.3, 6.5), it is difficult to be certain of the fine-scale comparative effects of additional impacts, including removing individuals for translocation. This was also true of projections under an imbalanced sex ratio; all models of all threat combinations with 75% male offspring, with and without removal of Group C, indicated a 100% chance of extinction (Figure 6.11), although time to extinction for the source population shortened by between 2-5 years after translocation (Figure 6.12). Indeed, under all scenarios, translocation of Group C slightly reduced persistence time of the source population.

Under a moderate catastrophe, extinction risk to the metapopulation (species) was also greater than that projected for the existing population at status quo, and similarly extreme under all other scenarios (Figure 6.11). Metapopulation persistence times were generally the same or slightly less than leaving the population at status quo in all scenarios (Figure 6.12). Together, these projections indicate that the translocation modelled here did not improve the outlook for the species. This is likely a result of the vulnerability of the newly established population. Although it was not the primary objective of this model to assess viability of the translocated population, it is clear that the new population established simply by transfer of three individuals (with no further supplementation) has a very high probability of extinction under both moderate and severe catastrophes ($PE \geq 0.97$, PE=1.00, respectively), even in the absence of other threats.

Under a biased offspring sex ratio, probability of extinction is also extreme (PE=1.00) under catastrophes of either severity. The persistence time of the translocated population was between 27-36 years under the moderate catastrophe scenario, and only 7-8 years if the population experiences a severe catastrophe.

Table 6.5 VORTEX PVA model results for effect on population viability of translocation as a potential management action, whereby a subset of individuals from the existing population (Population 1: source) are removed to establish a second population (Population 2: translocated). Viability measures (as per Table 6.3) given for each population and metapopulation (species). Grey shaded cells indicate scenarios in which 100% of simulated populations went extinct.

Hunting level	Habitat loss level	Catastrophe type	Sex Ratio at birth (%males)	Population	r_s	SD (r_s)	PE	N-extant	N-all	GD	TE
none	none	Moderate (typhoon)	50	Pop 1 (source)	-0.003	0.100	0.55	14.31	6.65	0.60	103.7
none	none	Moderate (typhoon)		Pop 2 (transloc)	0.003	0.155	0.97	10.96	0.31	0.42	36.3
n/a				Metapop (species)	-0.005	0.096	0.53	14.57	6.96	0.60	105.3
1 pair/10 years	none	Moderate (typhoon)	50	Pop 1 (source)	-0.016	0.115	0.94	11.67	0.74	0.62	80.8
none	none	Moderate (typhoon)		Pop 2 (transloc)	0.003	0.155	0.99	9.09	0.12	0.34	38.3
n/a				Metapop (species)	-0.017	0.110	0.93	11.28	0.86	0.58	86.0
none	-0.4% annually	Moderate (typhoon)	50	Pop 1 (source)	-0.006	0.110	0.80	6.66	1.60	0.50	104.4
none	none	Moderate (typhoon)		Pop 2 (transloc)	0.003	0.156	0.98	9.56	0.18	0.42	37.0
n/a				Metapop (species)	-0.007	0.106	0.78	7.10	1.78	0.51	106.4
1 pair/10 years	-0.4% annually	Moderate (typhoon)	50	Pop 1 (source)	-0.018	0.120	0.99	6.57	0.05	0.39	75.2
none	none	Moderate (typhoon)		Pop 2 (transloc)	0.003	0.154	0.98	9.64	0.23	0.46	38.0
n/a				Metapop (species)	-0.019	0.114	0.97	8.97	0.28	0.46	80.9
none	none	Severe (disease)	50	Pop 1 (source)	-0.102	0.303	1	-	-	-	17.7
none	none	Severe (disease)		Pop 2 (transloc)	0.013	0.261	1	-	-	-	7.7
n/a				Metapop (species)	-0.107	0.302	1	-	-	-	18.5
1 pair/10 years	none	Severe (disease)	50	Pop 1 (source)	-0.121	0.306	1	-	-	-	15.1
none	none	Severe (disease)		Pop 2 (transloc)	0.012	0.261	1	-	-	-	7.9
n/a				Metapop (species)	-0.123	0.304	1	-	-	-	16.0
none	-0.4% annually	Severe (disease)	50	Pop 1 (source)	-0.103	0.305	1	-	-	-	17.6
none	none	Severe (disease)		Pop 2 (transloc)	0.011	0.259	1	-	-	-	7.8
n/a				Metapop (species)	-0.106	0.300	1	-	-	-	18.4

1 pair/10 years	-0.4% annually	Severe (disease)	50	Pop 1 (source)	-0.121	0.305	1	-	-	-	15.2
none	none	Severe (disease)		Pop 2 (transloc)	0.010	0.261	1	-	-	-	8.2
n/a				Metapop (species)	-0.121	0.302	1	-	-	-	16.4
none	*none*	*Moderate (typhoon)*	*75*	Pop 1 (source)	-0.020	0.107	0.995	5.80	0.04	0.44	62.3
none	*none*	*Moderate (typhoon)*		Pop 2 (transloc)	0.007	0.164	0.999	5.00	0.01	0.50	27.6
n/a				Metapop (species)	-0.022	0.104	0.995	6.80	0.04	0.50	64.7
1 pair/10 years	*none*	*Moderate (typhoon)*	*75*	Pop 1 (source)	-0.028	0.112	1	-	-	-	41.8
none	*none*	*Moderate (typhoon)*		Pop 2 (transloc)	0.010	0.162	1	-	-	-	26.8
n/a				Metapop (species)	-0.029	0.109	1	-	-	-	46.7
none	*-0.4% annually*	*Moderate (typhoon)*	*75*	Pop 1 (source)	-0.020	0.109	0.997	4.00	0.02	0.48	61.0
none	*none*	*Moderate (typhoon)*		Pop 2 (transloc)	0.009	0.163	1	-	-	-	26.6
n/a				Metapop (species)	-0.022	0.106	0.997	4.00	0.02	0.48	63.5
1 pair/10 years	*-0.4% annually*	*Moderate (typhoon)*	*75*	Pop 1 (source)	-0.028	0.112	1	-	-	-	40.5
none	*none*	*Moderate (typhoon)*		Pop 2 (transloc)	0.009	0.164	1	-	-	-	27.0
n/a				Metapop (species)	-0.030	0.109	1	-	-	-	45.5
none	*none*	*Severe (disease)*	*75*	Pop 1 (source)	-0.102	0.298	1	-	-	-	16.4
none	*none*	*Severe (disease)*		Pop 2 (transloc)	0.011	0.265	1	-	-	-	7.6
n/a				Metapop (species)	-0.106	0.297	1	-	-	-	17.4
1 pair/10 years	*none*	*Severe (disease)*	*75*	Pop 1 (source)	-0.121	0.303	1	-	-	-	13.8
none	*none*	*Severe (disease)*		Pop 2 (transloc)	0.010	0.256	1	-	-	-	7.9
n/a				Metapop (species)	-0.123	0.301	1	-	-	-	15.1
none	*-0.4% annually*	*Severe (disease)*	*75*	Pop 1 (source)	-0.108	0.303	1	-	-	-	15.7
none	*none*	*Severe (disease)*		Pop 2 (transloc)	0.012	0.263	1	-	-	-	7.7
n/a				Metapop (species)	-0.111	0.300	1	-	-	-	16.7
1 pair/10 years	*-0.4% annually*	*Severe (disease)*	*75*	Pop 1 (source)	-0.120	0.302	1	-	-	-	13.9
none	*none*	*Severe (disease)*		Pop 2 (transloc)	0.014	0.256	1	-	-	-	8.0
n/a				Metapop (species)	-0.121	0.300	1	-	-	-	15.1

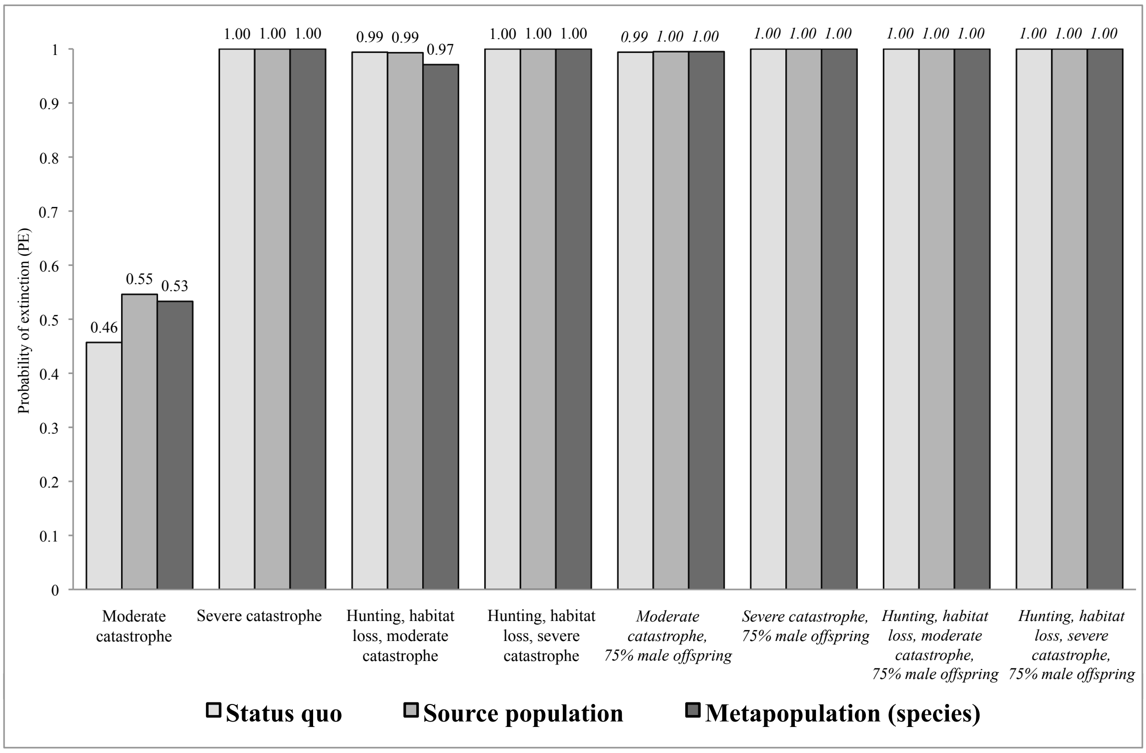


Figure 6.11 Projected probability of extinction (PE) under possible management scenarios: left at status quo (with risk of threats and catastrophe and no conservation action); and translocation whereby a subset of individuals from the existing population are removed to establish a second population, with different threat/catastrophe combinations – PE reported for source population and metapopulation (species). Identical scenarios but allowing for biased offspring sex ratio (75% male) indicated by *italics*.

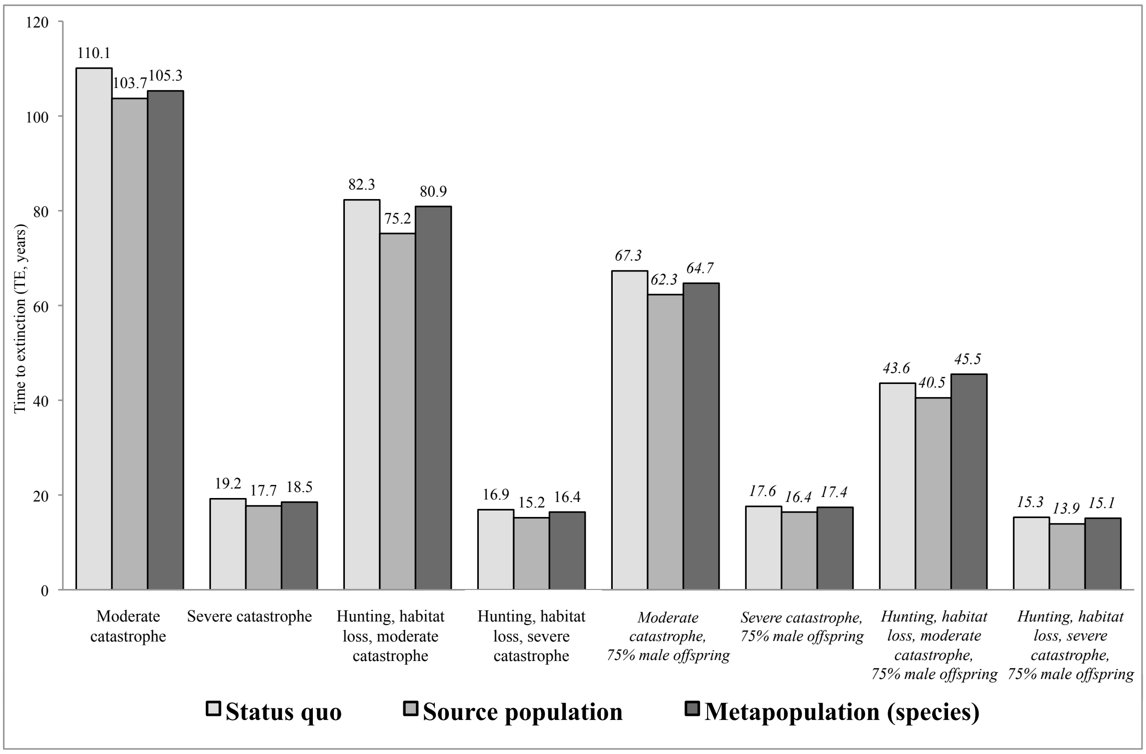


Figure 6.12 Projected mean time to extinction (TE, years) under possible management scenarios: left at status quo (with risk of threats and catastrophe and no conservation action); and translocation whereby a subset of individuals from the existing population are removed to establish a second population, with different threat/catastrophe combinations – TE reported for source population and metapopulation (species). Identical scenarios but allowing for biased offspring sex ratio (75% male) indicated by *italics*.

Discussion

Status quo: taking no proactive conservation action

The results of the PVA models developed in this study provide an evidence-base with direct insights for best-practice conservation planning for the Hainan gibbon. If the remaining population is left as is, with no active conservation management, it has a high probability of becoming extinct within the next 150 years. The probable time to extinction and likelihood of extinction are dependent upon the number and level of threats we consider the population to be subject to. Indeed, the value of PVA resides in comparison of quantitative metrics of population viability from a suite of models that emulate different scenarios (Akçakaya and Sjogren-Gulve 2000, Reed et al. 2002). Even in the absolute 'best-case' scenario, i.e. assuming the population is not subject to threats and not vulnerable to catastrophes, model projections indicate a 30% chance that it will go extinct within just over 100 years due to stochastic processes alone. This indicates that the species' intrinsic demographic limitations coupled with demographic, environmental, and genetic stochasticity may be sufficient to render the population vulnerable to extinction.

In the much more likely situation of at least the risk of some kind of catastrophe, the vulnerability of the population becomes extreme, with probability of extinction under a moderate catastrophe jumping to nearly 50% within 110 years, and a severe catastrophe forecast to be devastating for the species, reducing the projected population persistence to less than 20 years. This is still assuming the population is free from the threats of hunting and/or habitat loss, which is likely to be an overoptimistic assumption. If these threats are also taken into account, then likelihood of extinction rises and probable time to extinction shrinks further still under all scenarios. Even under only a moderate catastrophe, allowing for hunting and habitat loss indicates that there is a 99% chance the population will become extinct within the next 82 years. If the population's offspring sex ratio is biased, as molecular results from this study suggest (see Chapter 4), then the population may be extinct in less than 44 years, only 14 years longer than the time that has passed since Liu et al. (1984) called for the urgent conservation of the species. Furthermore, if the population does survive, it will only persist in tiny numbers (<10 individuals), with less than half of the population's current genetic diversity, which is already substantially reduced (again, see Chapter 4).

Comparative case studies show that under some environmental conditions, small populations can sometimes survive for protracted periods even in the absence of conservation actions. However this appears to rely upon the natural protection afforded by isolation and remoteness, or often good fortune. For example, the Lord Howe Island stick insect (*Dryococelus australis*) was thought to be extirpated from Lord Howe Island, Australia, by the 1920s as a result of *Rattus rattus* introduction, but in 2002 a small population of 24 individuals was located on a precipitous terrace 65m above sea level on a nearby tiny island (Balls Pyramid) in uncharacteristic, suboptimal habitat (Priddel et al. 2003). This may also be true of gibbon populations. Notably, *N. nasutus* was until recently feared extinct, but a single population was rediscovered along Vietnam's remote northern border in 2002 (La et al. 2002), and then across the border in China in 2006 (Chan et al. 2008). The current trans-boundary population is estimated at 110 individuals persisting in an isolated area of limestone forest (Dat et al. 2008). However, infrastructure development, hunting, and limited forest availability now threaten the survival of this and many other fragmented gibbon populations (Bach and Rawson 2011, Mootnick et al. 2012). Given the current level of human encroachment in BNNR (Chan et al. 2005), observed rate of habitat loss (Zhang et al. 2010), and inherent risk of catastrophe (Reed et al. 2003), the question is 'When will the Hainan gibbon's luck run out?' Together, the Hainan gibbon model results presented here indicate that if no proactive conservation interventions are implemented, unless existing threats can be removed and the population miraculously escapes natural disasters, the species is at a very high risk of extinction (60-100% probability) within 15-100 years.

Evidence for management actions

Demographic considerations

The level of mortality at dispersal is evidently a key factor that can alter the viability of the population. This supports concerns raised previously about this being a critical life stage, and so a probable limiting factor constraining population growth (Chan et al. 2005). When dispersal mortality was extremely high (50%), the population growth rate became acutely negative, indicating that the population would almost certainly rapidly decline to extinction if mortality gets this high, even in the absence of other threats. With lower dispersal age mortality, closer to that reported for other gibbon populations (15%; Traeholt et al. 2005), the risk of extinction reduced to 10%, and the growth rate was similar to that observed under a roughly doubled carrying capacity, indicating that managing the population to decrease mortality at this life stage could improve the species' outlook almost as much as providing additional habitat, assuming all threats are controlled.

It is clear that intrinsic factors will also determine the fate of the population. All available evidence indicates the reproductive rate used for all models was appropriate. Testing the IBI displayed by most other gibbon species (3 years: 33% females breeding) produced an extremely dire outlook for the population, with an alarmingly high probability of extinction, even in the absence of threats or catastrophes. The comparatively better viability measures observed assuming an IBI of 2 years suggests that the species' relatively short IBI, likely in combination with the apparent polygynous mating system, may have engendered a reproductive resilience that has allowed the population to persist for the last 30 years at such a low size and with low quality habitat of limited availability.

The species' sex ratio of offspring also altered viability projections starkly. Under a severe or even moderate bias, population vulnerability rose sharply, and it's resilience to threats was also compromised, with even the lowest level of each threat leading to alarmingly high extinction probabilities and shortened persistence times. Furthermore, under severe male-bias the modelled management actions did little to improve the viability of the species, indicating the population's capacity for recovery may be severely compromised if such a bias exists. A biased sex ratio may or may not be adaptive in mammals (Clutton-Brock and Iason 1986, Thogerson et al. 2013), including for gibbons (Jago and Melfi 2010), meaning it may be extremely challenging, if not impossible, to manage this factor directly. It is important that managers are aware of the impediment this condition may cause when considering the goals of any potential management actions.

Increased available habitat

Sensitivity testing revealed that increasing the carrying capacity of the habitat may have a positive influence upon the population's viability in an ideal situation (no threats). Models of different threat scenarios indicated that increasing the carrying capacity of BNNR by immediately doubling available habitat could improve the population's outlook, provided it is not subject to a severe catastrophe, the sex ratio at birth is balanced, and the threats of both habitat loss and hunting can be removed. Under the model specifying a moderate catastrophe only, probability of extinction was reduced to 13% within a mean time of 100 years following an immediate increase in available habitat. This was lower than the probability of extinction expected allowing for immediate habitat increase under the threats of hunting and moderate catastrophe (43%), compared to moderate catastrophe risk without habitat increase (46%), and the idealistic baseline model assuming no threats and no action (31%). It is clear, therefore, that any benefit to be gained by immediately increasing available habitat requires simultaneous management of existing deterministic threats to the population. Furthermore, Hainan gibbons were previously lost from adjacent forest patches within and outside BNNR, so before any immediate habitat increase could be achieved by reconnecting these patches, the drivers of these landscape-level losses must be addressed.

The other potential option for increasing available habitat will require intensive, costly reforestation of degraded patches and/or conversion of areas used for commercial plantations (pine, rubber etc.) within and adjacent to BNNR. Provided seedlings of appropriate tree species were immediately available for such efforts, available data indicate gibbons prefer habitats with high densities of large trees and high canopy cover/interconnectivity (Hamard et al. 2010), and probable forest maturation rates will mean a likely lag of 30-40 years before replanted forest can mature into structurally appropriate gibbon habitat (Aide et al. 2000, Phoonjampa et al. 2011). Under this scenario, assuming only the risk of moderate catastrophe, population viability only modestly improved, with roughly a 30% probability of extinction within about 100 years, equivalent to the level predicted under no threats, catastrophes or management actions. However, probability of extinction was still lower under delayed forest increase than the scenario in which no action was taken and the population was only vulnerable to a moderate catastrophe. This would suggest that increasing habitat, even if not achieved immediately, could improve the resilience of the population to a moderate catastrophe such as a typhoon, but again, only if other deterministic threats can be managed, and the sex ratio of offspring is balanced.

The habitat increase models produced are only a simple exploration of this possible management action. Practically, efforts required to increase existing habitat by 100% would likely necessitate a more complex strategy than either modelled here, for example a combination of reforestation and construction of canopy bridges until the forest matures. As a result, we might expect a real effect somewhere between the two model outcomes; an intermediate improvement in viability. However, these models also assume a one-off increase in habitat in 150 years. In reality, managers would likely strive to further increase available habitat in the future, within limits set by the land use surrounding the reserve. Therefore, such an approach might achieve a greater increase in population viability than observed in either model. Regardless of these limitations, these models serve to indicate that a one-off 100% increase to the existing carrying capacity of BNNR will likely only improve the outlook for the species if the threats of hunting and habitat loss can be removed, and the degree of improvement we might expect will also be dependent upon the intrinsic demographic limits of the population (sex ratio of offspring). Crucially, an increase in habitat appears to do nothing to safeguard the population from the impact of a major catastrophe, whether forest could be made available immediately or not. Under all scenarios in which severe catastrophe was included, increase in habitat did not decrease probability of extinction for the population or delay time to extinction, regardless of whether the population was also subject to other threats or not. However, this does not mean that an increase in habitat should not be attempted. While the risk of natural disaster is acute, the population appears to have avoided one to date, and population growth that may be permitted by increasing habitat could permit implementation of other actions which are presently not considered viable (e.g. establishment of a regular translocation regime; see below).

Translocation

Outputs from the translocation models strongly suggest that this management option cannot be implemented without considerable extinction risk to both the existing population and any translocated individuals. Under the simple translocation scenario modelled, the probability that the source population may go extinct was the same or higher than this probability without translocation for all catastrophes, threats and their modelled combinations. The same was true of the metapopulation, indicating that species viability did not improve under the translocation scenario. This suggests that even one translocation event may compromise the source population under the model assumptions made here. This is likely to be a result of the population's already tiny size; removing 12% of the population (three individuals) and so diminishing it further will only add to the instability experienced by such small populations as a result of both deterministic and stochastic factors. Clearly, the modelled scenario is a very basic representation of the translocation management action, with no further supplementation of the new population after the initial translocation event. It is therefore unsurprising that the translocated population became extinct in virtually all simulations under both moderate and severe catastrophes, as a population this small is liable to fall subject to stochastic processes very quickly (Fagan and Holmes 2006), demonstrated by the very short observed persistence times. The fate of this new population could perhaps be improved by moving these individuals into captivity (rather than another in-situ area), where risks of natural catastrophes could be avoided with careful husbandry and strict hygiene procedures etc. However it was beyond the scope of this analysis to investigate such a potential action.

Although gibbons rescued from the illegal pet trade and areas devastated by logging have been successfully reintroduced into the wild (Cheyne 2009), and rigorous release criteria have been proposed (Cheyne and Brulé 2004), rehabilitation and release of gibbons is still in its infancy (Cheyne et al. 2012). Examples of conservation translocations of gibbons are extremely scarce and have only consisted of emergency efforts to rescue stranded groups. Five family groups of eastern hoolock gibbons (*Hoolock leuconedys*) have been translocated from small, exceptionally fragmented, unprotected clusters of trees in Arunachal Pradesh, India, to an area inside Mehao Wildlife Sanctuary (The Times of India 2012). However, it is not yet clear whether this work can be regarded as a translocation 'success'. It is therefore challenging to determine an optimal translocation schedule for gibbon populations. It was clear from the hunting threat model that removal of one pair of individuals every ten years would greatly jeopardise the viability of the current population, both in isolation and when imposed in combination with other threats and catastrophes. This result is indicative of the population's fate, whether these animals are removed due to hunting or removed to supplement a new population. Therefore, it is difficult to imagine that a translocation programme regularly removing animals at this rate would be sustainable for the source population.

According to the IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN-SSC 2013, p. 20): “If removal of individuals from a source population causes a reduction in its viability in the short-term, the translocation objectives should include balancing this with the expected gain in viability of the destination population, so that the species has a greater overall viability than without the translocation, within a stated time period”. By this condition, translocation of just Group C and/or additional pairs is unlikely to be viable, and under the modelled conditions may be prohibitively risky to the species. However, this analysis constitutes an investigation of this potential conservation action solely from the scientific perspective, in an attempt to provide evidence to inform management decisions. Various additional stakeholder attitudes encompassing the political, social, and/or economic practicalities of such an action will be crucial to holistically evaluate both the level of risk to the existing population that we are willing to accept, and the overall feasibility of translocation as an appropriate action for the Hainan gibbon population.

Multiple conservation actions may be more likely to succeed

Within the increased habitat models, the best improvements to population viability occurred under situations in which the threat of hunting was also controlled. Inherently, these models assumed that habitat increase occurred under the condition that no additional loss of the existing or newly available habitat was experienced. For simplicity, translocation was modelled in isolation of other possible improvements that could be implemented, and was found to be very risky for the current source population and ineffectual in establishing a new population. If it is possible to increase available habitat, and control the threats of hunting and habitat loss, then this may change. The population may be able to reach a growth rate (even under stochastic processes and moderate risk of catastrophe) which could facilitate the regular removal of individuals from the source population and so permit a translocation programme. More complex modelling, if possible, will be required to ascertain if this case.

Limitations of model outputs

PVA models cannot definitively demonstrate the exact probability or time to extinction of a population, but constitute an analytical approach that can be used to indicate the likely fate of the population from the parameter values employed (Reed et al. 2002). As the assumptions of PVA models are relatively simple and based upon sound biological reasoning appropriate to long-lived mammals, the biases within the model (and so the model predictions) are relatively simple and more likely to underestimate rather than overestimate extinction risk (Traill et al. 2010). VORTEX model forecasts have been demonstrated to perform with impressive accuracy given adequate data. In a retrospective test, VORTEX PVAs using long-term datasets from 21 wild populations produced population decline risk predictions which closely matched observed outcomes (Brook et al. 2000). PVA outputs reported in this study are based upon the best available information for the species, further informed by data from other gibbon species and sensitivity testing for the impact of parameter inaccuracies. Most variables did not substantially alter model predictions, but those that did reveal important considerations for management. For these variables, the baseline values used in all models are likely to be accurate, as the baseline stochastic growth rate suggests very little growth potential as observed for the real population in recent years.

As sensitivity testing demonstrates, inaccuracy in demographic variables can alter predictions of population viability, making it important to obtain the most robust data possible for accurate model projections. However, this will always be a challenge for species of extreme rarity, especially shy, cryptic ones like the Hainan gibbon. Therefore, we must accept imperfect data and some model limitations if we are to attempt to act to conserve Critically Endangered species in time, given the speed of the global extinction crisis and the emerging effects of human-induced climate change (Lee and Jetz 2008, Traill et al. 2010). Indeed, in addition to the (necessary) limitations of individual models discussed previously, the effect of inbreeding, while incorporated into all models, may have been underestimated in this PVA. The pedigree used for the starting population specified the known parentage for only 36% of the current population, as it was not possible to determine the relationships (genetic or observationally inferred) of solitary individuals or those in the two non-habituated social groups. The model assumes the remaining 64% of animals are unrelated, which is unlikely to be the case. As the negative effect of lethal equivalents will only act upon inbred animals, underrepresenting the level of inbreeding will underestimate its effect upon population viability and thus may underestimate extinction risk. Therefore, the model results can be regarded as conservative rather than exaggerated predictions of the vulnerability of the species. This, however, only makes the predictions more alarming, given the high extinction probabilities and short periods to extinction projected under most scenarios. As such, these findings should be used as a starting point for additional investigation of the population's viability, or treated as potentially conservative estimates if used for evidence-based conservation planning for the species.

Next steps and future directions

The PVA conducted here is meant as a first step in the exploration of measures that may enhance or diminish the viability of the last Hainan gibbon population. Beyond the immediate insights that this analysis has provided into likelihood of Hainan gibbon extinction and priorities for the species' conservation, this PVA is intended as a platform for development of an expanded Population and Habitat Viability Analysis (PHVA) and other additional assessments for conservation planning. Indeed, the models constructed here have already served as a foundation for recovery strategy planning incorporating the input of gibbon researchers and conservation biologists carried out as part of the 2014 International Conservation Planning Workshop for the Hainan Gibbon (Cressey 2014). The sensitivity testing conducted within my study indicated that accurate data on the population's sex ratio of offspring at birth and level of female reproductive success (i.e. exact IBI) are vital to understanding the exact viability of the population and therefore the possible impact of any management strategies. Therefore additional data to support or refine values used and assumptions made here would enhance future modelling.

Future analysis should also explore additional potential conservation actions, including more complex multi-faceted actions that implement multiple management strategies simultaneously, and where possible, consider more expensive and intrusive actions, such as establishing a captive breeding programme from some/all of the existing population. Husbandry guidelines have been developed for the housing and captive breeding of *Hylobates moloch* (Campbell 2008), but few gibbon species are represented in existing captive-management programmes (Melfi 2012). It is unclear how well wild Hainan gibbons would fare in current ex-situ conditions, although three captive individuals of the species were successfully housed within London Zoological Gardens during the period from 1892 to 1911 (Flower 1892, Pocock 1905, Welch 1911, Flower 1929), when husbandry techniques and housing conditions were far less sophisticated. Furthermore, captive populations may avoid some of the extrinsic stochastic and deterministic threats a wild population faces. I was unable to explore this action here, due to limitations of the modelling program, so this remains to be assessed within other platforms, for example a decision-tree framework.

An informative next step would be to extend the models constructed here to build more a complex, multifaceted "metamodel" to incorporate the species' spatial considerations and additional genetic considerations (e.g. population genetic variability), along with threats like disease and climate change. Emerging 'next generation' conservation management metamodels, such as 'MetaModel Manager' (Pollak and Lacy 2013), allow several discrete models of different population aspects to be linked to assess extinction risk where threats are diverse, act at different spatial scales, or interact in a non-linear manner. These metamodels may be able to capture the complex behaviour of a population in more sophisticated ways than several separate individual models. Although this level of modelling was beyond the scope of this study, it remains a promising new approach that may assist in conservation planning for the Hainan gibbon in the near future.

Chapter 7. General Discussion

Thesis aim

With a single population of approximately 25 individuals, constrained to c. 15 km^2 of suboptimal habitat in one location, the Critically Endangered Hainan gibbon is the world's rarest ape and one of the world's most threatened mammal species. Targeted conservation actions are urgently required if we are to prevent the global extinction of this endemic Chinese/Hainanese mammal, a loss that would signal the first known extinction of any ape species in the Holocene Epoch. A lack of robust, empirical information and uncertainty regarding the species' basic biology has previously impeded an evidence-based approach to management of the population. Therefore, I aimed to develop a comprehensive evidence-base for the Hainan gibbon in order to permit informed conservation planning for the species. By adopting a multifaceted approach, I have generated crucial new baseline data for the Hainan gibbon which reveal important insights into key features of the ecology, behaviour and genetic status of the last surviving population, and the species' likelihood of survival under different management scenarios. This thesis represents the most comprehensive investigation of the species to date, and the first study to employ quantitative conservation planning tools to objectively assess the population's viability. The findings of this work therefore have crucial implications for effective conservation management of the species. My research also demonstrates the need to employ a suite of analytical approaches and the importance of methodological transparency when gathering data required for the informed management of species of extreme rarity.

Summary of key findings

Before endeavouring to derive a sound evidence-base for conservation planning, it is first necessary to assemble and assess the information available for a given species of conservation concern. This allows existing evidence for particular management actions to be evaluated comprehensively and objectively, and more fundamentally, permits identification of knowledge gaps to guide research. A critical review of the current evidence-base for the Hainan gibbon indicated that systematically-derived empirical data regarding the species' biology, ecology, behaviour and genetic status were severely lacking. Additional, rigorous investigation of the species' spatial requirements and genetic diversity, along with demographic parameters (relatedness, sex ratio) and possible intrinsic versus extrinsic drivers of key ecological and behavioural traits, was essential. Data on these specific features, and the population's potential response to manipulation of key parameters (mortality rates, extrinsic threats, available habitat), were required to address existing theories about possible factors constraining the species' recovery and appreciate potential management actions required to promote population survival and growth.

A principal objective of this thesis was to clarify fundamental characteristics of the Hainan gibbon's biology, ecology and behaviour, so that the role these factors may play in controlling recovery of the population could be better understood. Past authors raised concerns that an exceptionally large home range requirement in combination with limited available habitat within BNNR may be preventing population growth, and producing the notable group size and structure observed for the species (Liu et al. 1989, Jiang and Wang 1999, Wu et al. 2004, Zhou et al. 2008b). I therefore investigated the species' spatial requirements as a priority factor. Comprehensive reassessment of the home range of a Hainan gibbon social group revealed a yearly home range of 1-2 km^2, and a median estimate of 1.49 km^2. Approximately 0.71 km^2 (c. 50%) of the yearly home range is utilised by the group in both wet and dry seasons, with different parts of the landscape also being used in different seasons. Overlap between social group home ranges is between 6-17%. There was also some support for a preference for forest between elevations of 800-1,200 m a.s.l., as suggested by Liu and Tan (1990). Together, these new estimates provide no evidence for the species' home range being as large as the previously reported 9.9 km^2 (Zhou et al. 2008a, Zhou et al. 2008b, Li et al. 2010). Instead, by utilising a standard, transparent sampling methodology and a number of different analytical approaches, I was able to derive a robust estimate of the Hainan gibbon's home range that is consistent with estimates reported for other closely related crested gibbon species (*N. concolor, N. nasutus*) that are subject to the same pressures of small population size, limited available habitat and reduced habitat quality (Jiang et al. 2006, Fan and Jiang 2008a, Fan et al. 2010, Fan et al. 2013b). This revised estimate is of great importance as it suggests that home range and the amount of available habitat *per se* are alone unlikely to be constraining population growth, and that other factors (e.g. genetic relatedness, lack of available mates) may be responsible for the recent limited population recovery.

Although numerous authors (Liu et al. 1989, Zhou and Zhang 2003, Fellowes et al. 2008) have speculated that the species' precipitous past population decline may have produced a concomitant decline in genetic diversity and associated genetic consequences (e.g. inbreeding), to date little information has been available to clarify the genetic condition of the remaining population. I therefore conducted a comprehensive assessment of the species' current genetic diversity within the context of its past genetic diversity, and quantified key demographic parameters which have genetic implications (extent of inbreeding, sex ratio, relatedness). Using historical museum samples spanning the period 1899-1980, and faecal samples from 36% of the current population, I was able to demonstrate a significant temporal decline in diversity (heterozygosity and allelic richness) and significant differentiation of the current population from the historical samples using a number of standard metrics (F_{ST}, D_{est}, PCoA, Bayesian clustering analysis). Investigation of the species' temporal pattern of effective population size (N_e) revealed that the observed low level of genetic diversity in the current population does not represent a long-term pattern for the species but is the direct result of the recent past population bottleneck. This analysis also indicated that the population likely experienced an earlier decline by the start of the 20th century. This finding contributes important new molecular support for inferred declines (and loss) of gibbon populations observed during this period in mainland China, as well as populations of other mammal species in Hainan (van Gulik 1967, Dobroruka 1970, Wen 2009). I also revealed that individuals in the remaining population are, on average, related at the level of half- to full-siblings, which may lead to increased inbreeding and associated consequences in the near future. Molecular quantification of the sex of individuals in the current population indicated a substantial male-biased ratio of offspring (3 males : 1 female). These findings have important considerations for management, including expectations regarding possible rates of population recovery, and indicate that the genetic and demographic state of the population must be considered when contemplating potential conservation actions.

In the context of the traditional paradigm of gibbon ecology and behaviour, the remaining Hainan gibbon population reportedly shows markedly atypical patterns of home range size and social group organisation (Liu et al. 1987, 1989, Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b). To date, it has not been clear whether these traits represent typical characteristics for the species or a response to the population's presently compromised situation. I combined data from as many wild populations of gibbons as possible and used comparative methods within a phylogenetic framework to identify intrinsic versus extrinsic drivers of family-wide variation in these traits. I also tested whether the observed values for the Hainan gibbon are indeed unusual, relative to the rest of the Hylobatidae, by statistically comparing these observed values against values predicted by data from other gibbon populations. Strong, significant phylogenetic signals were apparent for home range, group size and mating system across gibbons. After controlling for these signals, predictive models indicated additional intrinsic and extrinsic correlates of some of these traits. Gibbon home range size was associated with group size and mating system, and site-level social group density. Social group size was associated with mating system and site-level mean annual rainfall. For the Hainan gibbon, group size, although large (>6 individuals on average), is in line with that predicted by the pattern of evolutionary relationships, as are the group sizes observed for all other gibbon species. However, Hainan gibbon home range, even when tested using my revised estimate, is larger than expected relative to other gibbon species, as are the home ranges observed for *N. concolor* and *N. nasutus*. While it was not possible to test the observed Hainan gibbon mating system against hylobatid-wide patterns in the same manner, there were no significant predictors of variation in this trait across the family other than the pattern of phylogenetic relationships. Together, these findings suggest that large, polygynous groups may be evolutionarily characteristic to both the Hainan gibbon and the most closely related *Nomascus* species. Hainan gibbon home range, by comparison, is seemingly being influenced by current extrinsic conditions. These patterns indicate that while the species' home range may change if the situation within BNNR can be modified, the complex, polygynous social structure (including resultant large group size) is unlikely to alter regardless of management action, and must be accommodated in any conservation planning. The results also offer an improved understanding of the drivers of these traits in the three basal *Nomascus* species, meaning that these conservation implications extend to the management of *N. concolor* and *N. nasutus* populations. Furthermore, by revealing some gibbon traits to be phylogenetically conserved and others to be more flexible, the findings of this comparative analysis contribute wider, fundamental insights into gibbon ecology and behaviour.

As a result of its tiny size, the sole surviving Hainan gibbon population is vulnerable not only to the external, deterministic threats which drove the population down to its present compromised state, but also to additional stochastic effects that create increased instability, and which can further depress population growth in small populations (Shaffer 1981, Soulé 1987). This means that even if the extrinsic threats to the population can be controlled, the species may still be at risk of extinction due to the inherent instability found in small populations. I conducted the first quantitative assessment of the vulnerability of the Hainan gibbon population within the context of the complex set of threats faced by extremely small populations. I used Population Viability Analysis to assess the species' relative viability under current conditions in BNNR and a number of potential threat and management scenarios. Assuming a best-case scenario, where the population is not subject to threats and not vulnerable to catastrophes, model projections indicated there is a 30% chance that the species will become extinct within just over 100 years due to stochastic processes alone. Under the more realistic expectation that the population is at risk of a catastrophic event with moderate impact, the probability of extinction increases to nearly 50%. If the known drivers of Hainan gibbon decline, hunting and habitat loss, are not controlled absolutely, there is a 99% chance the population will become extinct within the next 82 years. Models specifying a typical gibbon interbirth interval (IBI; 3 years), which is longer than that observed for the Hainan gibbon population (c. 2 years), revealed that the species' relatively short IBI in combination with the apparent polygynous mating system may have been a key factor that allowed the BNNR population to persist for the last 30 years, but will not necessarily prevent the species' extinction in the years to come. Incorporating elevated mortality at the age of dispersal from social groups and a male-biased sex ratio of offspring also revealed extremely high levels of extinction risk, indicating that these factors must be considered within conservation planning. Models directly exploring possible management actions indicated that mitigating external (deterministic) threats and doubling the available habitat may improve the species' viability. If such habitat increase could be achieved immediately (e.g. through enhanced canopy connectivity), the risk of extinction may lower substantially, but population viability will improve only modestly if purely methods that involve a time lag for forest maturation are employed. At present, it does not appear that translocation of a subset of the existing population to establish a second wild or captive population is viable. The tiny size of the surviving population means that removal of even just three individuals at present will severely compromise the source population and the species' survival. However, this is not to suggest that this action should not be investigated further, as theoretically, such a step may become viable in the future could the population size be increased.

Implications for Hainan gibbon conservation

Together, the analyses conducted in this study strengthen the evidence-base for Hainan gibbon conservation planning by providing comprehensive new baseline data on the species' ecology, behaviour, population genetics and population viability under possible management scenarios. Considering the data in combination, it is clear that leaving the population under current management conditions is not an advisable option. Endangered vertebrate species with low population sizes, long generation times and limited genetic variability, as revealed here to be the case for the Hainan gibbon, are very unlikely to adapt and survive anthropogenically-altered conditions without intervention (Vander Wal et al. 2013). Crucially, my direct, quantitative assessment of the species' long-term viability indicated that the Hainan gibbon is highly likely to go extinct in the near future without active conservation management, owing to its tiny population size. To avoid extinction, it will be necessary to address the issue of the species presently being reduced to a single, very small population. Therefore, managers must focus on strategies that will promote population growth in order to increase population size and, if possible, allow additional populations to be established. This is likely to require both immediate actions to improve survival and encourage population growth, and additional actions, that may only be possible after initial population growth is achieved, to establish one or more additional populations (e.g. translocation, *ex situ* management).

PVA indicated that enhancing the carrying capacity of available habitat could improve the growth of the population, but only if the extrinsic threats of hunting and habitat loss are controlled absolutely. Therefore, maintaining and improving current efforts to safeguard the population from these threats is crucial, e.g. strengthening the existing monitoring patrols, community awareness initiatives, and wider actions targeting poverty alleviation in surrounding communities. Clearly, increasing and improving the available habitat, using both methods that allow an increase to be achieved as soon as possible (linking existing fragmented habitat patches), and those that will enhance the quality and extent of the BNNR landscape longer-term (reforestation), will also be vital. However, the systematic evaluation of the Hainan gibbon's spatial requirements indicated that the species' home range is smaller than previously reported. Furthermore, although its home range is actually presently larger than predicted according to phylogenetic relationships alone, the detected correlates of hylobatid home range (group size, mating system, group density) indicate that the observed Hainan gibbon home range is unlikely to be the result of poor habitat quality and/or availability *per se*. As such, a lack of space (i.e. habitat) for new groups is unlikely to be solely accountable for the limited population growth observed to date, and simply managing the available habitat may not address all constraints to population growth.

My analysis also revealed important demographic and genetic considerations for the species which may play a role in population dynamics, and which further indicate that habitat enhancement alone may not be enough to ensure the survival of the Hainan gibbon. The level of relatedness between individuals in the remaining population is high: half- to full-siblings on average. While a general lack of comparative data from other gibbon populations makes it difficult to determine if this is higher than typical for gibbons, such a level may present inbreeding problems within only a few generations, if it has not done so already. Thus, to support long-term population growth, additional intensive measures, such as direct genetic management of the population (*in situ* or *ex situ* manipulation) and even genetic supplementation from a closely related species (e.g. as per Florida pander recovery efforts; Johnson et al. 2010) may be necessary. The current male-biased ratio of offspring may also impair future population growth. Evidence from captive populations suggests that the sex ratio of offspring in gibbons could be related to nutritional levels (Jago and Melfi 2010). This could mean that any offspring sex ratio bias in a wild population may be the result of poor habitat quality, which further supports the need for habitat improvement. However, if this demographic feature is the result of stochastic forces (chance variation in sexes born), rather than extrinsic conditions, habitat improvement may not directly resolve the present bias. This conclusion is clear from the dire predictions of the PVA models incorporating this bias, including those that simulated habitat increase.

Additional intensive measures beyond threat amelioration and habitat improvement will certainly be required if the species is to recover to more than one population in the future. The establishment of multiple populations will likely necessitate direct intervention whereby a subset of individuals is actively removed from the current population and translocated either to captivity or another (well-protected) floristically-suitable area in the wild. Rigorous reintroduction criteria exist for gibbons (Cheyne and Brulé 2004, Cheyne et al. 2012) and a number of family groups of *Hoolock leuconedys* have been translocated over short distances in India without incident (The Times of India 2012), indicating that this intensive management approach is feasible. The insights gained into the Hainan gibbon's complex social structure are especially important in this regard. It is evident that large, polygynous groups are usual for the Hainan gibbon. Consequently, any direct manipulation of the population, such as removal of individuals, must take this demography into account in order to minimise disturbance and maximise the chance of success.

The assessment of population viability under a simple translocation strategy indicated that this type of intensive intervention may be unfeasible at present due to the tiny population size. Nevertheless, this measure may become possible if population growth could be promoted, and further modelling (e.g. assessing removal of immature individuals rather than adults) is required to determine both the minimum population status at which this strategy may become viable, and the optimal translocation approach. It is also clear from the model predictions that a severe catastrophe will have devastating consequences for the population. As the surviving population suffers from reduced genetic diversity, the species may be more vulnerable to such impacts, including disease and rapid environmental changes. It is therefore crucial that an emergency response plan is developed that stipulates when (at what population size or composition threshold) and how (what actions) to respond to a catastrophic decline in population size. This may include moving the post-catastrophe population to another area or into captivity. Therefore, even if direct manipulation of the population is not to be attempted at present, the details (e.g. appropriate husbandry) of how to implement such a response should at least be discussed by managers. Increasing the capacity of the BNNR Management Office will also be important, particularly in terms of improving methods to monitor the population. Exact data on population size and composition are necessary if fine-scale changes in population size are to be detected. This information will be crucial to evaluating whether implemented measures are affecting the desired population increase and when to enact emergency mitigation actions. Consequently, investment to support the team responsible for the front-line management response will be vital to the success of any adaptive conservation management of the species.

While the species is presently extremely vulnerable, hope is not lost for the Hainan gibbon. As previous successful efforts to conserve species of extreme rarity demonstrate, with appropriate and adequate intervention, species can be brought back from the brink of extinction. The Chatham Islands black robin (*Petroica traversi*) and the Mauritius Kestrel (*Falco punctatus*) were each successfully recovered from a single pair of surviving individuals (Butler and Merton 1992, Jones et al. 1995). These species now number around 230 and 400 animals respectively (BirdLife International 2013a, b) as a result of intensive management efforts. Such recoveries are also possible for less fecund, longer lived mammal species. The northern elephant seal (*Mirounga angustirostris*), which is estimated to have declined to as few as 20 animals in the early 20th century, now numbers over 170,000 animals which have recovered naturally following strict laws protecting the species and its breeding colony range (Campagna 2008). The current population of Père David's deer (*Elaphurus davidianus*), constituting more than 53 herds of up to 10 individuals each (under captive management), was recovered via captive breeding from just 11 reproductive individuals (Jiang and Harris 2008). What these examples and my new baseline data for the Hainan gibbon indicate, is that multiple actions, both landscape-level management strategies and more intensive measures involving direct manipulation of the population to address demographic and genetic considerations, may be required to safeguard the future of the species.

Wider implications

As previous conservation successes (e.g. Chatham Islands black robin, Przewalski's horse *Equus ferus przewalskii*, golden lion tamarin *Leontopithecus rosalia*) and probable species and subspecies losses (e.g. po'ouli *Melamprosops phaeosoma*, baiji *Lipotes vexillifer*, dusky seaside sparrow *Ammodramus maritimus nigrescens*) have illustrated, when a species declines to just a handful of individuals, ecosystem-level management approaches alone are unlikely to be sufficient to prevent extinction (Groombridge et al. 2004). Additional factors come into play in tiny populations (reduced genetic diversity, demographic and environmental stochasticity, Allee effects) that mean intensive, tailored management actions are usually required to conserve species of extreme rarity. Detailed, objective, comprehensive population-specific information on a species' biology and population status is required to identify appropriate conservation actions. This study demonstrates that even for threatened species for which few data exist and collection of new data is difficult due to tiny sample sizes, by employing a suite of research techniques along with standardised, transparent methodology, it is possible to develop a robust evidence-base that can be used to identify new steps toward improved species conservation.

The outcomes of the individual analyses detailed in this thesis demonstrate their individual benefits for informing Hainan gibbon conservation management. Contextualising the species' current genetic diversity within the framework of its historical diversity revealed a loss of genetic diversity as a result of both recent and prolonged population decline. This adds to the body of evidence highlighting the importance of placing current genetic data within a historical context when considering the implications of genetic factors for conservation management of threatened species, especially species of extreme rarity (Groombridge et al. 2009, Raisin et al. 2012, Bristol et al. 2013). Additionally, I determined that placing a threatened species' current patterns of observed behaviour and ecology within a phylogenetic framework, and assessing correlates of such traits at a higher taxonomic order, can provide crucial insights into which traits may be responding to current extrinsic conditions and thus reveal targets for conservation management. This analysis also shows that the comparative approach can be applied to address single-species questions, not just questions across large taxonomic groups, which therefore has implications beyond conservation to broader evolutionary biology. Most importantly, my thesis displays the advantage of a multifaceted approach. Collecting multiple forms of biological data using contrasting scientific methods to derive a complementary and more complete picture of a threatened species can provide holistic insights which studies that focus on single issues (e.g. just genetic diversity or just habitat destruction) may fail to reveal, but which are required for effective conservation management (Crandall 2009, Gebremedhin et al. 2009). The power of combining ecological, behavioural, genetic and population status and population viability information derived from multiple analytical approaches is evident in the nuanced insights that the newly derived Hainan gibbon evidence-base has permitted into required management actions for this Critically Endangered species.

Adopting this approach for future studies of other species of extreme rarity could greatly inform conservation action for other urgently needed recovery programmes. For example, the Chinese crested tern (*Sterna bernsteini*) is estimated to number 30-49 mature individuals, and while external threats are well known, the species' breeding ecology, movements, genetic diversity, and extent of small population impacts remain poorly understood (Liu et al. 2009). Similarly, the Critically Endangered Cuban greater funnel-eared bat (*Natalus primus*) is now thought to number only 100 mature individuals which are restricted to a single cave (Cueva La Barca), making it extremely vulnerable to extinction (Tejedor et al. 2005). The species requires urgent conservation action; however, beyond protecting Cueva La Barca and its surroundings, additional potential actions required to secure the population have not been identified due to a lack of research and evidence (Mancina et al. 2007). Similarly, other gibbon species could also benefit from the holistic approach employed here. The sole surviving population of the Critically Endangered *N. nasutus* has received considerable research attention since its rediscovery in 2002, including studies into social structure and group dynamics (Fan et al. 2010), behaviour, feeding ecology and habitat preference (Fan et al. 2011a, Fan et al. 2012, Fei et al. 2012), and population viability under current conditions (Fan et al. 2013b). However, as yet there has been no known assessment of the possible response of the population to potential management techniques or investigation of its genetic condition. My study revealed that a severe population bottleneck can impact the genetic diversity of a gibbon population, and such analysis could greatly inform conservation management of *N. nasutus* as this population may also be suffering such impacts following its own acute bottleneck. There are also many other populations of Endangered and Critically Endangered gibbon species (particularly in Vietnam, Cambodia and Laos) which are declining and very poorly understood (Pollard et al. 2007, Rawson et al. 2011) for which this approach would be advantageous. These are just some of the many species for which the methods employed in this study to derive a comprehensive evidence-base could be applied to improve conservation planning.

Future directions

The robust and comprehensive evidence-base developed in this thesis is the first step on the road to recovery for the Hainan gibbon. Unfortunately, detailed biological data supporting specific recommendations of what needs to be done to conserve a species will not necessarily ensure conservation action. Conservation is a complex process that requires adequate resources and the commitment of responsible government bodies and other key stakeholders. Leadership, accountability, and rapid decision-making while there is still an opportunity to act, are all needed to minimise the loss of species worldwide (Martin et al. 2012). Without sufficient political will, robust science will do nothing. Despite calls for urgent action to conserve the Christmas Island pipistrelle (*Pipistrellus murrayi*) on the basis of evidence of rapid population decline (Lumsden et al. 2007, Lumsden and Schulz 2009), delays in government-level decision-making meant that when a decision was finally made (in 2009) to attempt to capture the remaining individuals and establish a captive breeding colony (first recommended in 2006), the species was already lost (Lumsden 2009). A striking similar story is true for the po'ouli, where delays in decision-making by the responsible agencies meant that efforts to promote breeding *in situ* and then establish a captive population also failed as they came too late (Groombridge et al. 2004, VanderWerf et al. 2006, Black et al. 2011).

The loss of these species is a poignant warning of the vulnerability of such populations and the danger of inaction. For the Hainan gibbon, where multiple stakeholders (including regional, provincial and national governmental authorities, national and international NGOs, and inhabitants of surrounding villages) have differing perspectives and motivations, there is also a risk that the complex attitudinal landscape may impede responsive conservation action. If all parties involved do not recognise the problem and the need for urgent action, and do not attempt to work together, there is a risk that the Hainan gibbon may go the way of other Chinese endemics such as the baiji and Père David's deer, and two other gibbon species in China, *H. lar* and *N. leucogenys*. The recent International Conservation Planning Workshop for the Hainan Gibbon (March 2014; Cressey 2014), which brought together representatives from all groups with vested interests, is a vital step in ensuring productive collaborative relationships that foster action. The recommendations of this meeting (to be produced mid-2014) will be vital to galvanise action at number of levels.

I strongly urge that the following conservation actions be implemented and additional research be undertaken as a priority to further inform conservation management and ensure the future survival of the Hainan gibbon:

- Control, and if possible eliminate, the threat of hunting absolutely. This will require numerous actions, including: greater legal protection for other mammal species in BNNR, to create a disincentive for poaching of those animals (as well as gibbons) and minimise the indirect threat that such hunting presents to gibbons; community education and support to reiterate the need to protect gibbons directly, and emphasize the importance of other mammals to a healthy forest ecosystem; poverty alleviation efforts to improve livelihoods in villages neighbouring BNNR, to reduce the need to harvest animals and other non-timber forest products (NTFP) from BNNR.

- Prevent further degradation of the remaining habitat within BNNR through community education initiatives to make the local community aware of the impact of NTFP harvest and other human disturbance upon the entire BNNR ecosystem, including gibbons.
- Increase the available gibbon habitat using short- and long-term methods: trial (install and monitor) canopy bridges to connect fragmented areas within BNNR to determine if the Hainan gibbon population will use such apparatuses and thus whether this approach is feasible; carry out additional forest restoration within the reserve, and (where appropriate) in degraded areas between BNNR and nearby protected areas (e.g. Erxianling National Nature Reserve).
- Assess gibbon ranging patterns against underlying habitat features to identify the primary environmental drivers of Hainan gibbon ranging to further guide habitat restoration efforts (including suitability assessment of potential areas for future actions, e.g. translocation).
- Expand genetic analysis by employing Next Generation Sequencing techniques (which permit assessment of a larger number of genomic sites and thus increased data resolution) to validate findings of limited genetic diversity and relatedness levels in the surviving population.
- Trial new methodologies to enhance population monitoring, such as bioacoustic monitoring and thermal imaging, to improve detection of fine-scale population changes (e.g. group composition), and obtain more accurate data on the survival rates of dispersing and solitary individuals.
- Investigate the feasibility of other potential management strategies, including: establishing a captive population from all or some of the current population, to establish a secure population in conditions tailored to promote successful breeding; and more complex actions that implement multiple management strategies in a staggered approach (e.g. habitat improvement followed by translocation). Risks, benefits and potential outcomes can be explored using PVA, meta-models, decision trees, and other quantitative decision-making tools.

- Develop an emergency response plan of action that details when (at what population size limit) and how (what actions) to deal with a catastrophic event that results in extreme and rapid population decline. This will require exploration and ranking of possible appropriate response options which can be informed by additional research into the feasibility of a captive breeding programme and other *in situ* and *ex situ* actions.

By adopting this integrated approach, in association with bold and pro-active decision-making, it will hopefully prove possible to save the Hainan gibbon from extinction. In the face of the current unprecedented rate of global biodiversity loss and the rapidly increasing number of threatened species, a science-based conservation strategy that draws upon many and varied lines of research and evidence is likely to become increasingly integral to conservation planning, to prevent the loss of species, especially those of extreme rarity.

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Appendix A. Details of UK Hainan gibbon historical museum specimens.

Details of specimen upon which Thomas (1892) described the species:

According to Thomas, this was the first specimen of the species to be sent to Europe, although Swinhoe had given a written account of the species in 1870 (Swinhoe 1870). The specimen was presented to the British Museum (Natural History) by W.T. Lay. It is assumed this occurred in 1891, based on the accession date of the Natural History Museum (NHM) specimen. The animal was reportedly shipped live from Hainan to Lay, and he subsequently kept it in captivity for 4 years in China. Thomas gives no indication of when or where the animal died, when or where the specimen was prepared, or who prepared it, before the specimen was presented to the British Museum (Natural History). Therefore, it is unclear how old the animal was when it was taken from the wild in Hainan, or when it died, when and in what form it travelled to the UK, or if in fact the specimen was alive for any time at all after leaving China. The specimen is listed as ‘juvenile’ in the NHM Catalogue of Primates.

Details of Hainan gibbons kept at London Zoo: from Flower (1892, 1929), Pocock (1905), and Welch (1911)

Male: Housed from 1892-1893 (As per NHM accession date). Presented to the Zoological Society of London (ZSL) by Mr Julius Newman on 26 July, 1892 (Flower 1892, Flower 1929). “The most noticeable acquisition during the month was a young Gibbon from Hainan, South China, of a uniform black colour, belonging to the species recently described by Mr Oldfield Thomas as *Hylobates hainanus*. The Society are indebted to Mr Julius Neumann, of Hoihow, Hainan, China, for this interesting animal, which is new to the Collection” (Flower 1892). The first representative of the species in the Gardens of the ZSL (Flower 1929). Referenced later as male by Welch (1911).

Died in captivity 1893?

Female: Housed from 1904-1907 (As per NHM accession date). Deposited at the ZSL 26 January 1904 by Mr. E. H. de St Croix: “female specimen of the Hainan Gibbon”. St Croix “procured her in the island of Hainan on July 11th, 1897” (Pocock 1905). The animal was believed by “natives” to be 6 weeks old at the time of her capture, although Pocock believed she was older as St Croix indicated she was weaned and “capable of fending for herself in the matter of food”; he estimated her approximate date of birth as 1897 (Pocock 1905). Thus, she was over 6 years old when she was given to London Zoo. Pocock observed that she began menstruating at the end of December 1903 and took this to mark her maturation to adult “when about seven years”. This constitutes the first life history data recorded for the species. Pocock (1905) detailed the menstruation of this animal and compared it to that of other apes (chimpanzee) and gibbon species, as well as other primates (*Ceropithecidae*). Based on (erroneous) observations of the animal’s reproductive anatomy made by St Croix and related to Pocock, he noted the (apparently common) mistake of “...determining females as castrated males on account of the unusual length of the clitoris in these Apes...”. Pocock documented the pelage colour change of this individual, which he reported occurred about six weeks after she arrived in London, and a few weeks after she was brought to the Zoo, i.e. at more than 6 years of age and at maturity (as indicated by the onset of menstruation). At length Pocock concludes that this “canescence”, as he terms it, is only exhibited by the females of the species, based on observations of mature black males in Hainan related to him by St Croix, and the accounts published by Swinhoe (1870) from local gazetteers that “the male is black and the female is white”. He noted the “coincidence between the appearance of menstruation and that of the colour change” allowing him to allude to (but not attribute the change to) an ontogenic explanation and infer that perhaps “it is characteristic of the species to change from black to grey at maturity”.

This is likely the first written account of this ontogenically driven change in fur colouration in this species, and possibly the earliest observation of this phenomenon for any other gibbon or primate species. Indeed Pocock remarks: “But, so far as I am aware, it was not previously known that a given individual after reaching maturity may change in colour in the way exemplified by Mr de St. Croix’s specimen”. He defended the distinction of the species, based on differences he observed in the hair of *hainanus* and *concolor* and rebuts Matschie’s claim; “…it is, in my opinion, premature to state without qualification that *hainanus* is a synonym of *concolor*.” Pocock also provided a detailed physical description of the species, noting the difference between this species and others he had observed, notably the texture of the hair and the crested head hair, as well as the difference of the Hainan gibbon’s voice in comparison to that of the Hoolock. He also described some simple behaviours of the species (namely drinking and action and bipedal abilities), and its ‘cry’ including a possible representation of it (many ‘hoo’s with upward inflections), and the “…ordinary expression or anger or remonstrance… a prolonged and guttural grunt”.

Died in captivity 1907 according to NHM specimen label.

Male: Housed from 1907-1911 (As per NHM accession date). Presented to the ZSL by R. Douglas Esq. on 6 December 1907. “One Hainan gibbon (*Hylobates hainanus*), male, from Hainan…” (Bradford 1908). No account of sex or further information regarding provenance, age etc. “A male of the rare *H. Hainanus* from Hainan…” (Welch 1911). Welch (1911) was aware of the mistakes made previously regarding the sex of *Hylobates* “on account of the large clitoris being mistaken for the penis" and was certain about the sex of this specimen: "I have made careful examination of all the specimens and am certain that the sex is as I have stated." Observations were made on the species of this individual by Welch (1911) of: male's genitalia, general physique of species and comparison of these feature and crown hair to those of other gibbon species housed at the Society's Gardens the time (namely *H. hoolock*, *H. agilis*, and *H. leuciscus*, and *Symphalangus syndactylus*).

Died in captivity 1911 according to NHM specimen label.

Details of Hainan gibbon kept at Dublin Zoo:

Information sourced by Geraldine Breen (c/: Nigel Monaghan of Natural History Division of national Museum of Ireland, April 2010) from the Royal Zoological Society of Ireland reports 1895-1899.

Male: Housed 1895-1899 (as per RZSI reports).

1895 report: "Hainan Gibbon (*Hylobates hainanus*), Habitat- China. Purchased 27th September 1895", but no information regarding from whom the specimen was purchased or its history i.e. its geographic origin beyond 'China', or how it arrived in Europe. It appears Dublin Zoo were very fond of this gibbon as it was a "unique specimen" and was "the second Anthropoid of its kind exhibited in the UK. No European has ever seen this species in its native haunts, although in 1893 one lived for some months in the London Gardens". The specimen was described as having a "gentle and confiding disposition" and as an "exceedingly rare and valuable specimen". According to Dr. Eugene Dubois the Hainan Gibbon "is more nearly related to man than any other ape".

1896 report: "...gibbon in best of health and spirit".

1898 report: "...need new enclosures....badly ventilated and insanitary". During the winter the specimen "suffered from repeated attacks of a mild febrile disease, closely resembling influenza".

1899 report: "... after nearly 5 years in zoo....gibbon is dead....zoo very upset because it also loses a Chimpanzee" (from the reports it suggests that the gibbon and chimp were inmates). "…Zoo and public had become very attached to the Anthropoids."

Died in captivity in 1899.

Appendix B. Summary of past research investigating the biology, ecology, behaviour, and population size of the Hainan gibbon to date, by study and by year (of reported data).

Study	**Year(s) of reported data**	**Species name**	**Aim(s)/Purpose of study**	**Effort**	**Collected new data?**	**Data reported**
Liu et al. (1984)	Early 1950s	*Hylobates concolor conolor, Hylobates hainanus*	no information	no information	yes (historical data through interviews)	Population estimate
Zhou et al. (2005)	1950-1964	*Nomascus hainanus*	a) examine decline of population in terms of changes in environment ecology and demography of Hainan; b) investigate 'current' population distribution and social structure	Surveyed 14 sites in 'core area' and three sites in 'buffer zones' of the reserve, plus an additional 13 potential sites outside reserve. No indication of number or duration of survey sessions (effort).	yes (historical data through interviews)	Population estimate (also cite Liu et al. 1984)
Zhou et al. (2005)	1964-1978	*Nomascus hainanus*	As detailed above	As detailed above	yes (historical data through interviews)	Population estimate (also cite Liu et al. 1984)
Liu et al. (1989)	late 1970s	*Hylobates concolor hainanus*	no information	no information	no	Population estimate (cite Liu et al. 1987)
Liu and Tan (1990)	1978	*Hylobates concolor hainanus*	no information	no information	no	Population estimate
Liu et al. (1984)	1978	*Hylobates concolor conolor, Hylobates hainanus*	no information	no information	yes (unclear if/how authors collected)	Population estimate
Liu et al. (1987)	1978	*Hylobates concolor hainanus*	no information	no information	no	Population estimate
Liu et al. (1989)	1978	*Hylobates concolor hainanus*	no information	no information	no	Population estimate
Zhou et al. (2005)	1978-1983	*Nomascus hainanus*	As detailed above	As detailed above	yes (historical data through interviews)	Population estimate (also cite Liu et al. 1984)
Liu et al. (1984)	1983	*Hylobates concolor conolor, Hylobates hainanus*	no information	no information	yes (unclear if/how authors collected)	Population estimate, group size, anecdotal behavioural data, birth rate, available habitat
Tan (1985)	1983	*Hylobates concolor*	Review of status of Chinese primates	no information	No	Population estimate (cite Liu et al. 1984), available habitat

Liu et al. (1989)	1984	*Hylobates concolor hainanus*	Preliminary study of ecology and behaviour of remaining population	5 days/month (total: 60 days/year) for 5 years	Yes	Population estimate, group composition
Zhou and Zhang (2003)	1984	*Hylobates concolor hainanus*	Recommendation of conservation strategies only	no information	No	Population estimate
Liu and Tan (1990)	1984-1985	*Hylobates concolor hainanus*	Investigate change in abundance, relate gibbon habitat use to vegetation type (abundance and diversity of food plants)	10 days (2x5 days)/month, total: 120 days/year. Observations of 'group A' for focus, three other groups for auxiliary observation. No indication of effort used to determine population estimate provided.	Yes	Population estimate, anecdotal behavioural data, home range, habitat preference, diet composition (spp. list)
Zhou et al. (2005)	1984-1995	*Nomascus hainanus*	As detailed above	As detailed above	yes (historical data through interviews)	Population estimate (also cite Liu et al. 1984, Zhang and Sheeran 1993, Zhang et al. 1995)
Wang and Quan (1986)	1986	*Hylobates concolor concolor*	Review of primate status in China only	no information	No	Population estimate (not referenced)
Bleisch and Chen (1990)	1987	*Hylobates concolor hainanus*	Investigate ecology and behaviour of black crested gibbons (*Hylobates concolor*) of Yunnan province	no information	No	Population estimate (cite Liu et al. 1987), anecdotal evidence of polygyny
Liu et al. (1987)	1987	*Hylobates concolor hainanus*	Aims not detailed (but seems status/population size update)	Paper reports one visit to BWL, but figures and social group composition appear to be based on observations by Liu from previous work	Yes	Population estimate, group size, group composition, anecdotal behavioural data, anecdotal evidence of polygyny
Liu et al. (1989)	1987	*Hylobates concolor hainanus*	As detailed above	As detailed above	Yes	Population estimate, group composition
Tan and Poirier (1988)	1987	*Hylobates concolor hainanus*	Review of primate status in China only	no information	No	Population estimate (not referenced)
Ma et al. (1988)	c.1988	*Hylobates concolor hainanus*	Taxonomy of southern Chinese gibbons (using museum specimens)	no information	yes (morphometric only)	Population estimate (not referenced)
Zhou and Zhang (2003)	1988	*Hylobates concolor hainanus*	Recommendation of conservation strategies only	no information	No	Population estimate
Liu et al. (1995)	1987-1989	*Hylobates concolor hainanus*	Quantify home range, habitat choice/use and seasonal patterns of these	160 days total. Gibbon activity and location (i.e. zone 1-9 only, not coordinates) recorded every 15 minutes. Direct observations of one group (of seven individuals) only.	Yes	Group size, home range, habitat preference

Liu et al. (1989)	1989	*Hylobates concolor hainanus*	As detailed above	As detailed above	Yes	Population estimate, group size, group composition, descriptive behavioural data, evidence of polygyny, birth rate, home range, available habitat, diet composition (spp. list)
Zhang (1992)	c. 1989	*Hylobates concolor hainanus*	Comment on status of species only	no information	No	Population estimate (not referenced)
Zhang (1992)	1992	*Hylobates concolor hainanus*	Comment on status of species only	no information	yes (unclear if/how authors collected)	Population estimate
Zhang and Sheeran (1993)	1993	*Hylobates concolor hainanus*	Update status of species	no information	Yes	Population estimate
Zhou and Zhang (2003)	1994	*Hylobates concolor hainanus*	Recommendation of conservation strategies only	no information	No	Population estimate
Wang (1995)	1995	*Hylobates concolor hainanus*	Report on status	No information of years/days/search effort, but small qualifying statement: "The wardens in the Nature Reserve could only try the best to monitor around the area and did limited research work."	Yes	Population estimate, group size, group composition, anecdotal evidence of polygyny
KFBG (2001)	1998	*Hylobates concolor*	Rapid biodiversity assessment of BNNR only	No information regarding effort used to derive population estimate; biodiversity survey: 6 days.	Yes	Population estimate, group composition, anecdotal behavioural data
Zhou and Zhang (2003)	1998	*Hylobates concolor hainanus*	Recommendation of conservation strategies only	no information	No	Population estimate
Wu et al. (2004)	2000	*Nomascus* c.f. *nasutus hainanus*	Determine status of species	no information	Yes	Population estimate, group size, group composition,
Fellowes et al. (2008)	2002	*Nomascus hainanus*	Population monitoring	no information	Yes	Population estimate, group size, group composition,
Wu et al. (2004)	2002	*Nomascus* c.f. *nasutus hainanus*	Determine status of species	91 days (294 person days); Nov-Dec 2001: 20 days (71 person days), 11 transect lines, total 69.5km; Feb-April 2002: 71 days (223 person days) point counts at listening posts. Gibbons detected (visual or aural) in 5/11 transect lines; from posts gibbons located 16 times at five sites.	Yes	Population estimate, group size, group composition, anecdotal evidence of polygyny, home range, available habitat
Zhou et al. (2008a)	2002	*Nomascus hainanus*	Report "inter-group encounters" i.e. details of interactions between social groups	Two social groups tracked by two teams. Report field observation period of September 2002-2006. No further indication of effort used to derive social group composition.	Yes	Group size, group composition, behavioural data

Zhou et al. (2008b)	2002	*Nomascus hainanus*	Document the mating and reproductive behaviours of the species, and reproductive biology (gestation period, interbirth interval etc.)	Social groups tracked by teams of two. Report fieldwork period of August 2002-January 2006, but subsequently describe 29-month field study with observations over 232 days (total: 7 months), accumulated total: 548.5 hours of direct observations. No further information regarding effort used to determine population estimates.	Yes	Group size, group composition
Zhou and Zhang (2003)	2003 ("now")	*Hylobates concolor hainanus*	Recommendation of conservation strategies only	no information	No	Population estimate, available habitat, diet composition (spp. list)
Chan et al. (2005)	2003	*Nomascus* c.f. *nasutus hainanus*	Status survey: A comprehensive, rapid survey of the species.	Survey conducted over 16 days over two stages. Stage one: 11 days at 16 listening posts in "old reserve" area; Stage two: 5 days, 13 teams surveyed "extension" area.	Yes	Population estimate, group size, group composition, anecdotal evidence of polygyny, home range (cite Liu et al. 1989, Liu and Tan 1990), habitat preference, available habitat (cite Liu et al. 1989), diet composition (spp. list)
Zhou et al. (2005)	2003	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Population estimate, group size, group composition, descriptive behavioural data, anecdotal evidence of polygyny, home range, available habitat, diet composition (spp. list)
Zhou et al. (2008a)	2003	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data
Zhou et al. (2008b)	2003	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Population estimate (cite Chan et al. 2005, Geissmann and Chan 2004, Zhou et al. 2005), group size, group composition
Zhou et al. (2008a)	2004	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data
Zhou et al. (2008b)	2004	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data, reproductive parameters
Zhou et al. (2008a)	2005	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data

Zhou et al. (2008b)	2005	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, emigration data
Lin et al. (2006a)	2006? (not stated)	*Nomascus hainanus*	To examine habitat quality in terms of food availability for gibbons, as well as the characteristics of food plant distribution.	No information	Yes	Population estimate (not referenced),available habitat, diet composition (spp. list)
Zhou et al. (2008a)	2006	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data
Zhou et al. (2008b)	2006	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Population estimate, group size, group composition, anecdotal evidence of polygyny, birth rate, home range, available habitat, diet composition (spp. list)
Mootnick et al. (2007)	2007	*Nomascus hainanus*	Review of 25 most endangered primates	no information	No	Population estimate
Fellowes et al. (2008)	2007	*Nomascus hainanus*	Assessment of status of species (through review of progress of population monitoring and other priority actions)	Population estimates from daily monitoring of gibbons (over 2002-2007 including periods of cessation lasting months). Home range estimates based months of direct tracking ‘daily’ over 2002-2004.	Yes	Population estimate, group size, group composition, birth rate, emigration rate, home range, habitat preference, available habitat, diet composition (spp. list)
Zhou et al. (2008a)	2007	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Group size, group composition, behavioural data
Zhou et al. (2008a)	2007? (unclear)	*Nomascus hainanus*	As detailed above	As detailed above	Yes	Population estimate, group size, group composition, behavioural data, anecdotal evidence of polygyny, emigration data, home range
Li et al. (2010)	2009	*Nomascus hainanus*	Survey of the (surviving) population's genetic diversity through study of genetic diversity of one social group (B)	35 scat samples in total collected from six individuals from one social group (B) - at least five replicates of each individual. 30 samples (86%) amplified successfully.	Yes	Population estimate, group size, anecdotal evidence of polygyny, birth rate (cite Zhou et al. 2008b), home range, available habitat (cite Zhou et al. 2005), genetic data

Appendix C. Ethogram of behavioural categories used to record behaviours observed during ranging activity of Hainan gibbon social groups.

Behavioural category	Description
call	vocalisation in form of stereotypical solo or duet song of species (not alarm call or grunting vocalisations)
feed	animal in process of inspecting, picking, ingesting or masticating a food item, as observed instantly, i.e. doesn't include movements between feeding sites ('Travel') or inactive periods during a "feeding bout" ('Rest')
groom (self)	running fingers or teeth through own fur, washing, smoothing or scratching own fur with tongue, teeth, hands, feet
groom (conspecific)	running fingers or teeth through fur of conspecific, washing, smoothing or scratching conspecific's fur with tongue, teeth, hands, feet
move	local movement of an individual at a location i.e. within a location from tree to tree, branch to branch etc., not moving over a distance ('travel'))
play	individual or individuals engaged in manipulation of objects (e.g. stick) or movement which is apparently 'purposeless' (i.e. no apparent immediate need or outcome is linked to behaviour -excluding the likely learning or social development outcomes of the behaviour, which are long-term), or interacting in non-aggressive or mock-aggressive way (e.g. chasing, biting, tussling)
rest	no displacement of body or active behaviour such as feeding, grooming etc.; eyes may be open or closed but animal is not active
travel	movement through the landscape, i.e. across a distance (e.g. to new location), usually at great speed , and often but not always involving most of the social group

Appendix D. An assessment of Hainan gibbon behaviour during ranging.

Group B spent the majority of its time making small-scale movements around a single locality, resting, or feeding, with these three behaviours collectively accounting for 72% of the total behaviours observed (Figure D.1). Other behaviours, including 'social' behaviour (conspecific grooming, self-grooming and play) occupied less time. As the group was less visible when moving at speed, the amount of time spent travelling may be under-represented. The majority of feeding time was spent eating fruit (over 86%), with other food types (leaves, flowers and invertebrates) consumed less frequently (Table D.1). These behavioural data are typical of daily activity patterns seen in other gibbons (as per Chivers et al. 2013), notably the closely related Cao Vit gibbon (*Nomascus nasutus*) (Fan et al. 2012). This indicates that there is unlikely to be any substantial bias in the Hainan gibbon ranging data, and they should be representative of typical home range use.

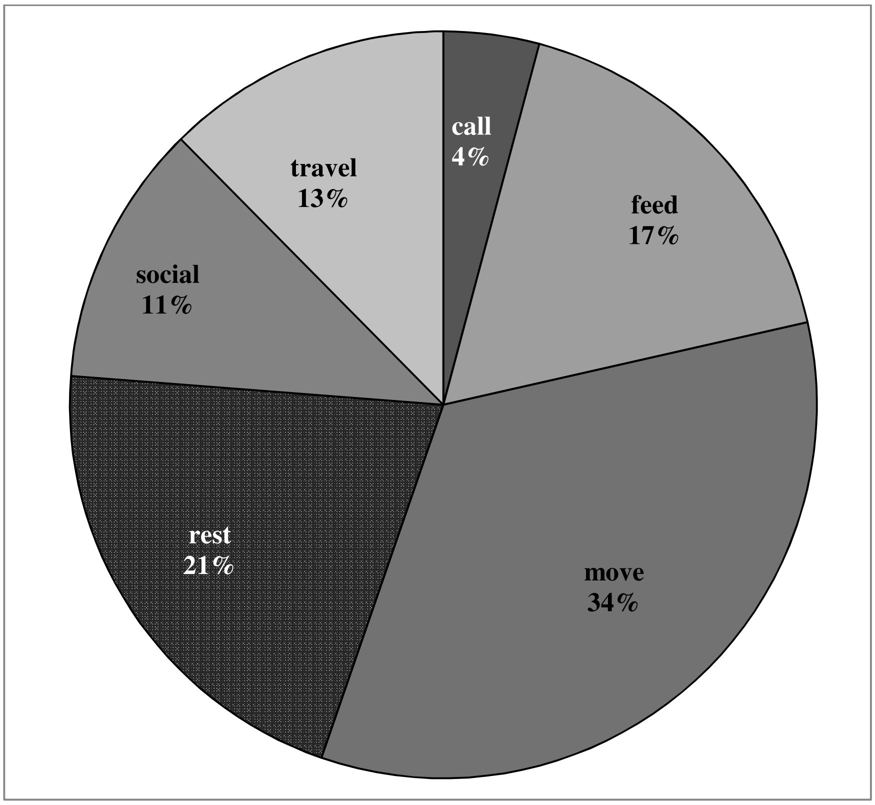

Figure D.1 Activity budget of Group B as per behaviours observed during ranging within BNNR (breakdown based upon percent of total observed instances over all observations).

Table D.1 Breakdown of frequency of consumption of different food types during 'feeding' behaviour observed during Hainan gibbon ranging.

Food type	**Observed instances**	**Proportion of observed instances**
fruit	58	86.6%
flower	1	1.5%
leaves	5	7.5%
invertebrate	1	1.5%
Total feeding instances	**67**	**100%**

Appendix E. Indices of independence of Hainan gibbon group location datasets collected for home range analysis.

Dataset	**Sample size (*n*)**	**Schoener index**[*]	**Swihart & Slade index**[*]
A_dry season	6	2.03	0.25
A_wet season	4	1.61	-0.05
A	10	***1.28***	0.32
B_dry season	106	***0.34***	***2.12***
B_wet season	102	***0.10***	***2.87***
B	208	***0.18***	***2.61***
C (wet season only)	30	***0.76***	***1.83***

[*] Values in ***bold italics*** indicate significant autocorrelation i.e. Schoener indices <1.6 or >2.4, and/or Swihart and Slade indices: >0.6.

Appendix F. An assessment of the accuracy of the ASTER GDEM V.2-derived contour dataset: difference (metres) between elevations reported via GPS and elevation of the nearest contour for a subset of locations (12 key geographic locations used during fieldwork).

Waypoint (location)	**Waypoint elevation (m)**	**Nearest contour or mid-point (when between two) (m)**	**Difference (m)**
Shan Ji Lu	1040	1050	10
Da Shi Tao	936	920	16
Ling Ba Gang	1242	1220	22
Ding Zi Gang	1017	995	22
A&B Listengang	1204	1195	9
A Listenpost 1	1110	1105	5
A Listenpost 2	955	940	15
C Listenpost	843	835	8
Shi Zi Lu Camp (B)	785	895	110
Qingsong Camp (A)	837	860	23
Fu Tou Ling Trig	1436	1405	31
Miao Villiage	475	485	10
Minimum difference			**5**
Maximum difference			**110**
Average difference			**23.42**
Standard Error (difference)			**8.18**

Appendix G. Gibbon field data survey: questionnaire for collection of population-level data of gibbon species at research sites directly from research groups and field teams.

Note: data from many fields within the below survey were not included in the comparative dataset and analyses due to poor response rates and data quality issues for those fields.

GIBBON FIELD SITE SURVEY, 2013

Introduction

Thank you very much for taking the time to complete this survey, I am grateful for any insights you can provide. The aim of this survey is to capture data for as many gibbon species from as many sites as possible, particularly information on the condition and disturbance of the sites occupied by gibbon populations, and population-specific data which may be currently unpublished. This data will be used to conduct a comparative analysis of the gibbons in order to determine the contribution of a number of intrinsic and extrinsic factors to key population variables. It is designed to inform a broader assessment of the factors of particular conservation concern for the Critically Endangered Hainan gibbon, and as such improve conservation management recommendations for this species.

Survey instructions

Please enter data for an individual gibbon species at the level of study site, that is, one population of one species at one site. If you have data on more than one gibbon species and/or more than one study site (even for the same species), please complete a separate survey for each one. Please try to enter as many values as possible, and provide estimates where necessary; please only select "don't know" for values you are truly unsure of.

Questions:

1. For the data you are reporting please indicate the:
   - Gibbon species (Latin name)
   - Study site name, county/province and country
   - Geographic coordinates (in decimal degrees N/S and E/W) of the study site
   - Elevation range which the gibbons occupy at site (min-max elevation, metres above sea level)
   - Your email address (only to associate a contact with the data)

2. Please provide estimates of the following attributes for this species at this study site (please enter "don't know" if you do not have this data):

- Home range (km^2) (average, and any observed upper and lower estimates)
- Social group size (average, and any observed upper and lower estimates)
- Total number of social groups at site (estimated no. of social groups)
- Total "closed" population at the site (estimated no. of individuals)
- Social group density (no. of social groups/km^2)
- Population density (individuals/km^2)
- Observed mating system (MONOGAMOUS = one breeding male and one breeding female; POLYGYNOUS = evidence of multiple females in social group with young simultaneously but only one breeding male)

3. Please indicate which of the following WWF Ecoregions (vegetation type/s) are found at the site (for details: http://worldwildlife.org/biome_categories/terrestrial-ecoregions):

- IM0102 Borneo lowland rain forests
- IM0103 Borneo montane rain forests
- IM0104 Borneo peat swamp forests
- IM0105 Brahmaputra Valley semi-evergreen forests
- IM0106 Cardamom Mountains rain forests
- IM0107 Chao Phraya freshwater swamp forests
- IM0108 Chao Phraya lowland moist deciduous forests
- IM0109 Chin Hills-Arakan Yoma montane forests
- IM0117 Irrawaddy moist deciduous forests
- IM0119 Kayah-Karen montane rain forests
- IM0121 Luang Prabang montane rain forests
- IM0126 Meghalaya subtropical forests
- IM0127 Mentawai Islands rain forests
- IM0131 Mizoram-Manipur-Kachin rain forests
- IM0132 Myanmar coastal rain forests
- IM0136 Northern Annamites rain forests
- IM0137 Northern Indochina subtropical forests
- IM0139 Northern Thailand-Laos moist deciduous forests
- IM0140 Northern Triangle subtropical forests
- IM0141 Northern Vietnam lowland rain forests
- IM0144 Peninsular Malaysian montane rain forests
- IM0145 Peninsular Malaysian peat swamp forests
- IM0146 Peninsular Malaysian rain forests
- IM0147 Red River freshwater swamp forests
- IM0149 South China-Vietnam subtropical evergreen forests
- IM0152 Southern Annamites montane rain forests IM0153 Southwest Borneo freshwater swamp forests
- IM0157 Sumatran freshwater swamp forests
- IM0158 Sumatran lowland rain forests
- IM0159 Sumatran montane rain forests
- IM0160 Sumatran peat swamp forests

- IM0161 Sundaland heath forests
- IM0163 Tenasserim-South Thailand semi-evergreen rain forests
- IM0164 Tonle Sap freshwater swamp forests
- IM0165 Tonle Sap-Mekong peat swamp forests
- IM0167 Western Java montane rain forests
- IM0168 Western Java rain forests
- IM0169 Hainan island monsoon rain forests
- IM0202 Central Indochina dry forests
- IM0205 Irrawaddy dry forests
- IM0210 Southeastern Indochina dry evergreen forests
- IM0211 Southern Vietnam lowland dry forests
- IM0303 Northeast India-Myanmar pine forests
- IM0304 Sumatran tropical pine forests
- IM0401 Eastern Himalayan broadleaf forests
- IM0402 Northern Triangle temperate forests
- IM1001 Kinabalu montane alpine meadows
- IM1402 Indochina mangroves
- IM1404 Myanmar Coast mangroves
- IM1405 Sunda Shelf mangroves
- PA0102 Yunnan Plateau subtropical evergreen forests
- PA0516 Nujiang Langcang Gorge alpine conifer and mixed forests
- Other WWF Ecoregion/s not listed above (please specify) [box for value]
- Don’t know

4. Please rate the quality/condition of the forest at the site (as per ITTO tropical forest condition classes*):

- **PRIMARY FOREST** = never subjected to human disturbance or so little affected that structure, functions and dynamics have not changed beyond natural elastic capacity of the ecosystem (Note: includes forests used by indigenous/local communities with traditional lifestyles consistent with conservation and sustainable use of biodiversity)
- **MANAGED PRIMARY FOREST** = primary forest where sustainable wood/non-wood harvesting, wildlife management, other uses have changed forest structure and species composition from original primary forest, but major goods and services are maintained
- **DEGRADED PRIMARY FOREST** = primary forest where initial cover has been adversely affected by the unsustainable harvesting of wood/non-wood forest products such that structure, processes, functions and dynamics are altered beyond the short-term resilience of the ecosystem (i.e. capacity of forest to recover from exploitation in near to medium term has been compromised)
- **SECONDARY FOREST** = woody vegetation re-growing on land that was largely cleared of original forest cover (i.e. carried <10% of the original forest cover), commonly develops naturally on land abandoned after modification
- **DEGRADED FOREST LAND** = former forest land severely damaged by excessive harvesting of wood/non-wood forest products, poor management,

repeated fire, grazing, other disturbances, such that inhibits or severely delays the re-establishment of forest after abandonment

- **PLANTED FOREST** = forest stand that has been established by planting or seeding (e.g. afforestation, reforestation, enrichment planting)
- Don't know
- **MIXTURE** of above forest condition classes (please specify classes)

* I.T.T.O (2002). ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. ITTO Policy Development Series No 13, International Tropical Timber Organization in collaboration with the Centre for International Forestry Research (CIFOR), the Food and Agriculture Organization of the United Nations (FAO), the World Conservation Union (IUCN) and the World Wide Fund for Nature (WWF) International.

5. Please rate the extent of degradation at the site: what percentage (approximately) of the forest at the site has been degraded by any type of human disturbance (logging, grazing etc.)? (Note: here, ‘degraded’ refers to forest showing reduced structure, function, species composition and/or productivity):

- Not degraded
- Less than 10%
- >10% - 25%
- >25% - 50%
- >50% - 75%
- >75% -90%
- More than 90%
- Don’t know
- Exact extent/level of degradation known -please specify (%)

6. Please provide an estimate of the amount of available, suitable habitat at the site (i.e. contiguous area of forest suitable for use by the gibbon species, *not* the size of the reserve/park in which the gibbons are found):

- Less than 1km^2
- 1-10 km^2
- >10-50 km^2
- >50-100 km^2
- >100-250 km^2
- >250-500 km^2
- >500-800 km^2
- >800-1,000 km^2
- >1,000-2,500 km^2

- >2,500-5,000 km^2
- >5,000-8,000 km^2
- >8,000-10,000 km^2
- >10,000/15,000 km^2
- More than 15,000 km^2
- Don’t know
- Exact size of available habitat known -please specify (km^2)

7. Please answer the questions below and provide associated data pertaining to hunting of the gibbon species at the site
(please enter "don't know" if you do not have this data):

- Is there evidence that the gibbon species is presently hunted at the site? (Y/N/Don’t know)
- If YES, please provide an estimate (if possible) of the current intensity of this on-going hunting (approx. no. gibbons hunted/year).
- Is there evidence that the gibbon species was hunted at the site in the past? (Y/N/Don’t know)
- If species was hunted at site in past but is no longer hunted, please indicate (if possible) the last record of hunting incident of the species at the site (approx. year).

8. Please answer the questions below and provide associated data pertaining to large-scale logging (commercial or illegal) at the site
(please enter "don't know" if you do not have this data):

- Is there evidence of large-scale logging, resulting in loss of gibbon habitat, currently being conducted at the site? (Y/N/Don’t know)
- If YES, please provide an estimate (if possible) of the current intensity of this on-going logging activity (approx. km^2 forest lost/year).
- Is there evidence large-scale logging was historically carried out at the site, resulting in loss of gibbon habitat? (Y/N/Don’t know)
- If site was logged in past but is no longer logged, please indicate (if possible) the last record of such logging at the site (approx. year).

9. Please answer the questions below and provide associated data pertaining to (legal or illegal) large-scale forest clearance for agriculture (crops, plantations, livestock grazing), and/or development (road construction, urbanisation) at the site:

a. Is there evidence of large-scale forest clearance associated with agricultural expansion and/or developmental incursion, resulting in loss of gibbon habitat, currently being conducted at the site? (Y/N/Don't know)
b. If YES, please provide an estimate (if possible) of the current intensity of this on-going forest clearance for agricultural expansion/developmental incursion (approx. km^2 forest lost/year).
c. Is there evidence large-scale forest clearance associated with agricultural expansion and/or developmental incursion, resulting in loss of gibbon habitat, was historically carried out at the site? (Y/N/Don't know)
d. If the forest at the site was cleared for agricultural expansion/developmental incursion in past but is no longer, please indicate (if possible) the last record of such large-scale clearance at the site (approx. year).

10. Please answer the questions below and provide associated data pertaining to small-scale human disturbance (e.g. NTFP collection) at the site:

- Is there evidence that small-scale human disturbance (e.g. NTFP collection) is presently degrading the gibbon habitat at the site? (Y/N/Don't know)
- If YES, please provide an estimate (if possible) of the current intensity of this on-going small-scale human disturbance (approx. tonnes NTFP harvested/year).
- Is there evidence that small-scale human disturbance (e.g. NTFP collection) historically degraded the habitat at the site? (Y/N/Don't know)
- If small-scale human disturbance was an issue at site in past but is no longer an issue (in terms of habitat degradation), please indicate (if possible) the last record of such disturbance at the site (approx. year).

Final request

Thank you once again for taking the time to complete this survey and for any data you have kindly been able to provide. If you have any additional information, including relevant REPORTS, PUBLISHED or UNPUBLISHED LITERATURE, or OTHER MATERIALS which may contain the above information, or ADDITIONAL RELEVANT DATA (e.g. estimates of population density and social group density at the site; data pertaining to other forms of disturbance, such as mining, dam development etc., at your site) which you are happy to share with me, or if you are willing to talk further about your data, please do get in touch.

Appendix H. Sources of gibbon comparative data for three response variables (home range, group size, mating system) by species and site (gibbon population).

Species	Site	Site location	Home range reference(s)	Group size reference(s)	Mating system reference(s)
Hoolock hoolock	Bangladesh1	Lawachara (NP), West Bhanugach Reserve Forest, Maulavibazar	Islam and Feeroz (1992), Österberg (2007)	Islam and Feeroz (1992), Österberg (2007)	Islam and Feeroz (1992), Österberg (2007)
Hoolock hoolock	India1	Bherjan Borajan Padumoni Wildlife Sanctuary, Assam	Jayanta Das (pers. comm., April 2013)	Jayanta Das (pers. comm., April 2013)	Jayanta Das (pers. comm., April 2013)
Hoolock hoolock	India2	Dehing Patkai Wildlife Sanctuary, Assam	Jihosuo Biswas (pers. comm., June 2013)	Chivers et al. (2013), Jihosuo Biswas (pers. comm., June 2013)	Jihosuo Biswas (pers. comm., June 2013)
Hoolock leuconedys	India3	Mehao WLS, Arunachal Pradesh	Jihosuo Biswas (pers. comm., June 2013)	Chivers et al. (2013), Jihosuo Biswas (pers. comm., June 2013)	Jihosuo Biswas (pers. comm., June 2013)
Hoolock leuconedys	China1	Nankang Park, Gaoligongshan Nature Reserve, Yunnan	Zhang et al. (2014)	Fan et al. (2011b)	Fan et al. (2011b), Chivers et al. (2013)
Hoolock leuconedys	Myanmar1	Mahamyaing wildlife sanctuary, Sagaing Division	Brockelman et al. (2009)	Brockelman et al. (2009)	Brockelman et al. (2009)
Hylobates abbotti	Malaysia4	Lanjak Entimau Wildlife Sanctuary, Sarawak	Rowe and Myers (2011)	Rowe and Myers (2011)	Rowe and Myers (2011), Chivers et al. (2013)
Hylobates agilis	Malaysia1	Sungai Dal, Gunong Bubu Forest Reserve, Malay Peninsular	Gittins (1980, 1982)	Gittins (1980), Leighton (1987)	Gittins (1980, 1982)
Hylobates agilis	Indonesia1	Kulai Tanang, Kerinci Seblat National Park, Jambi, Sumatra	Yanuar (2007)	Yanuar (2007)	Yanuar (2007)
Hylobates agilis	Indonesia2	Way Canguk Research Area, Bukit Barisan Selatan National Park, Lampung Province	Alice Elder (pers. comm., April 2013)	Alice Elder (pers. comm., April 2013)	Alice Elder (pers. comm., April 2013)
Hylobates albibarbis	Indonesia3	Gunung Palung National Park, West Kalimantan	Andrew Marshall (pers. comm., April 2013)	Marshall et al. (2009), Andrew Marshall (pers. comm., April 2013)	Andrew Marshall (pers. comm., April 2013), Chivers et al. (2013)

Hylobates albibarbis	Indonesia4	Sabangau, Central Kalimantan	Susan Cheyne (pers. comm., April 2013)	Hamard et al. (2010), Susan Cheyne (pers. comm., April 2013)	Chivers et al. (2013), Susan Cheyne (pers. comm., April 2013)
Hylobates funereus	Indonesia12	Kutai, Kalimantan	Chivers (1984)	Leighton (1987)	Chivers (1984)
Hylobates funereus	Indonesia13	Kayan Mentarang National Park, Kalimantan	Nijman and Menken (2005)	Nijman and Menken (2005)	Chivers et al. (2013)
Hylobates klossii	Indonesia5	Paitan River area, Siberut Island, West Sumatra	Whitten (1982)	Whitten (1982), Leighton (1987), Chivers et al. (2013)	Chivers et al. (2013)
Hylobates klossii	Indonesia6	Pungut Field Station, Peleonan Forest, Siberut, West Sumatra	Marcel Quinten (pers. comm., April 2013)	Quinten et al. (2010), Höing et al. (2013)	Marcel Quinten (pers. comm., April 2013)
Hylobates lar	Malaysia2	Tanjong Triang, Johore	Leighton (1987)	Leighton (1987)	Ellefson (1974)
Hylobates lar	Malaysia3	Kuala Lompat, Krau Game Reserve, Pahang	Chivers (1984)	Leighton (1987)	Raemaekers (1979)
Hylobates lar	Thailand1	Khlong Sai study site, Khao Yai National Park, Nakhon Nayok	Suwanvecho and Brockelman (2012)	Warren Brockelman (pers. comm., June 2013)	Suwanvecho and Brockelman (2012)
Hylobates lar	Thailand2	Mo Singto site, Khao Yai National Park, Nakhon Nayok	Bartlett (2009)	Warren Brockelman (pers. comm., June 2013), Ulrich Reichard (pers. comm., April 2013)	Brockelman and Srikosamatara (1984), Chivers et al. (2013), Warren Brockelman (pers. comm., June 2013)
Hylobates moloch	Indonesia7	Gunung Halimun-Salak National Park, West Java	Kim et al. (2011a)	Kim et al. (2011a)	Sanha Kim (pers. comm., April 2013)
Hylobates moloch	Indonesia8	Cagar Alam Leuweung Sancang Nature Reserve, Java	Malone (2007), Malone and Fuentes (2009)	Malone (2007), Malone and Fuentes (2009)	Malone and Fuentes (2009)
Hylobates moloch	Indonesia9	Turalak, Ujung Kulou, Java	Chivers (1984), Kappeler (1984)	Chivers (1984), Kappeler (1984)	Chivers et al. (2013)
Hylobates moloch	Indonesia10	Sokokembang forest, Central Java	Arif Setiawan (pers. comm., April 2013)	Arif Setiawan (pers. comm., April 2013)	Arif Setiawan (pers. comm., April 2013)
Hylobates muelleri	Indonesia11	Sungai Wain Protection Forest, Balikpapan, East Kalimantan	Vincent Nijman (pers. comm., April 2013)	Gilhooly (2012), Vincent Nijman (pers. comm., April 2013)	Susan Cheyne (pers. comm., April 2013), Vincent Nijman (pers. comm., April 2013)
Hylobates pileatus	Thailand1	Khlong Sai study site, Khao Yai National Park, Nakhon Nayok	Suwanvecho and Brockelman (2012)	Warren Brockelman (pers. comm., June 2013)	Suwanvecho and Brockelman (2012), Chivers et al. (2013)
Hylobates pileatus	Thailand3	Khao Ang Rue Nai Wildlife Sanctuary, Chachoengsao Province	Rungnapa Phoonjampa (pers. comm., April 2013)	Phoonjampa et al. (2011), Rungnapa Phoonjampa (pers. comm., April 2013)	Rungnapa Phoonjampa (pers. comm., April 2013)

Hylobates pileatus	Thailand4	Khao Soi Dai, Khao Khitchakut District	Srikosamatara and Brockelman (1987)	Leighton (1987), Brockelman and Srikosamatara (1993)	Brockelman and Srikosamatara (1984), Srikosamatara and Brockelman (1987)
Nomascus annamensis	Cambodia1	Veun Sai-Siem Pang Conservation Area, Stung Treng and Ratanakiri Province	Ben Rawson (pers. comm., April 2013)	Ben Rawson (pers. comm., April 2013)	Ben Rawson (pers. comm., April 2013)
Nomascus concolor	China2	Dazhaizi, Wuliang Mt., Jingdong County, Yunnan	Fan and Jiang (2008a,b), Fan Peng Fei (pers. comm., April 2013)	Fan and Jiang (2010), Fan Peng Fei (pers. comm., April 2012)	Fan et al. (2006), Fan and Jiang (2008a,b), Fan Peng Fei (pers. comm., April 2013)
Nomascus concolor	China3	Xiaobahe, Wuliang Mt., Zhenyuan County, Yunnan	Jiang et al. (1999)	Sheeran (1993), Jiang et al. (1999)	Haimoff et al. (1986, 1987), Bleisch and Chen (1991), Jiang et al. (1999), Fan et al. (2006)
Nomascus gabriellae	Vietnam1	Cat Tien National Park, Dong Nao	Marina Kenyon (pers. comm., April 2013)	Marina Kenyon (pers. comm., April 2013)	Marina Kenyon (pers. comm., April 2013)
Nomascus hainanus	China5	Bawangling National Nature Reserve, Baisha and Changjiang, Hainan	This study	Zhou et al. (2008a,b), this study	Liu et al. (1987, 1989), Bleisch and Chen (1991), Wu et al. (2004), Zhou et al. (2008b), this study
Nomascus leucogenys	Laos1	Nam Kading National Protected Area, Bolikhamxay Province	Julia Ruppell (pers. comm., April 2013)	Julia Ruppell (pers. comm., April 2013)	Julia Ruppell (pers. comm., April 2013)
Nomascus nasutus	China4	Bangliang, Jingxi County, Guangxi	Fei et al. (2012), Chivers et al. (2013), Fan Peng Fei (pers. comm., April 2013)	Fan Peng Fei (pers. comm., April 2013)	Fan et al. (2010), Fan Peng Fei (pers. comm., April 2013)
Nomascus siki	Laos1	Nam Kading National Protected Area, Bolikhamxay Province	Rowe and Myers (2011)	Chris Hallam (pers. comm., April 2013)	Chris Hallam (pers. comm., April 2013)
Symphalangus syndactylus	Malaysia3	Kuala Lompat, Krau Game Reserve, Pahang	Raemaekers (1979)	Gittins and Raemaekers (1980)	Gittins and Raemaekers (1980)
Symphalangus syndactylus	Indonesia1	Kulai Tanang, Kerinci Seblat National Park, Jambi, Sumatra	Yanuar (2007)	Yanuar (2007)	Yanuar (2007)
Symphalangus syndactylus	Indonesia2	Way Canguk Research Station, Lampung Province, Sumatra	Susan Lappan (pers. comm., April 2013)	O'Brien et al. (2004), Susan Lappan (pers. comm., April 2013)	Tim O'Brien (pers. comm., April 2013), Susan Lappan (pers. comm., April 2013)

Appendix I. Global multiple regression linear mixed-effects kinship models incorporating all significant predictors (*P*<0.05) from separate single regression models for a) home range and b) group size.

a) Home range global model (residual error: 0.114)

Fixed effect parameter estimates

Coefficient	**Estimate**	**SE**	**z-value**	***P*-value**[*]
(Intercept)	1.65	0.63	2.63	**0.0085**
group size	0.95	0.43	2.24	**0.025**
group density	-0.11	0.05	-2.24	**0.025**
mating system (1=polygyny)	0.24	0.12	1.89	0.059
annual mean temperature	-0.01	0.01	-0.81	0.420
annual precipitation	-0.12	0.17	-0.74	0.460

Random effects

Variance explained by phylogeny (%)	99.15%
Variance explained by within-species variation (%)	0.85%
Total variance explained:	9.84E-05

b) Group size global model (residual error: 0.043)

Fixed effect parameter estimates

Coefficient	**Estimate**	**SE**	**z-value**	***P*-value**[*]
(Intercept)	0.64	0.25	2.51	**0.012**
mating system (1=polygyny)	0.16	0.04	4.25	**0.00002**
home range	0.11	0.06	2.07	**0.039**
annual precipitation	-0.12	0.06	-2.04	**0.042**
annual mean temperature	0.01	0.00	1.4	0.160
latitude	0.00	0.00	-0.16	0.870

Random effects

Variance explained by phylogeny (%)	18.55%
Variance explained by within-species variation (%)	81.45%
Total variance explained:	2.51E-08

[*] Significant *P*-values in **bold**.

Appendix J. Ranking of home range candidate models (representing all possible combinations of the five predictors in the global model) by AICc, along with relative log-likelihood (RLL), ΔAICc, and model Akaike weights (w_i).

Candidate model	RLL	AICc	ΔAICc	w_i
1	1.00	-36.79	0.00	0.21
2	0.69	-36.06	0.73	0.15
3	0.62	-35.84	0.95	0.13
4	0.43	-35.08	1.71	0.09
5	0.32	-34.49	2.30	0.07
6	0.21	-33.68	3.11	0.04
7	0.19	-33.45	3.35	0.04
8	0.18	-33.42	3.38	0.04
9	0.17	-33.29	3.50	0.04
10	0.16	-33.16	3.63	0.03
11	0.14	-32.83	3.96	0.03
12	0.13	-32.68	4.11	0.03
13	0.10	-32.09	4.70	0.02
14	0.08	-31.82	4.97	0.02
15	0.08	-31.82	4.98	0.02
16	0.06	-31.02	5.77	0.01
17	0.04	-30.22	6.58	0.01
18	0.03	-29.98	6.81	0.01
19	0.03	-29.85	6.94	0.01
20	0.03	-29.73	7.06	0.01
21	0.03	-29.55	7.24	0.01
22	0.01	-28.08	8.71	0.00
23	0.00	-23.89	12.90	0.00
24	0.00	-23.28	13.52	0.00
25	0.00	-17.93	18.87	0.00
26	0.00	-16.37	20.43	0.00
27	0.00	-16.29	20.50	0.00
28	0.00	-15.24	21.56	0.00
29	0.00	-13.30	23.49	0.00
30	0.00	-10.51	26.28	0.00
31	0.00	-7.95	28.84	0.00

Appendix K. Ranking of group size candidate models (representing all possible combinations of the five predictors in the global model) by AICc, along with relative log-likelihood (RLL), ΔAICc, and model Akaike weights (w_i).

Candidate model	RLL	AICc	ΔAICc	w_i
1	1.00	-111.89	0.00	0.32
2	0.81	-111.46	0.43	0.26
3	0.43	-110.18	1.70	0.14
4	0.37	-109.90	1.99	0.12
5	0.12	-107.72	4.16	0.04
6	0.07	-106.63	5.26	0.02
7	0.05	-106.04	5.85	0.02
8	0.05	-105.73	6.16	0.01
9	0.04	-105.28	6.61	0.01
10	0.04	-105.22	6.67	0.01
11	0.03	-104.74	7.15	0.01
12	0.03	-104.74	7.15	0.01
13	0.03	-104.66	7.23	0.01
14	0.02	-104.26	7.63	0.01
15	0.02	-103.74	8.15	0.01
16	0.01	-102.74	9.15	0.00
17	0.00	-95.90	15.99	0.00
18	0.00	-95.64	16.25	0.00
19	0.00	-94.09	17.80	0.00
20	0.00	-93.95	17.94	0.00
21	0.00	-93.91	17.98	0.00
22	0.00	-93.90	17.99	0.00
23	0.00	-92.11	19.78	0.00
24	0.00	-91.95	19.94	0.00
25	0.00	-86.42	25.47	0.00
26	0.00	-85.90	25.99	0.00
27	0.00	-84.61	27.28	0.00
28	0.00	-84.43	27.45	0.00
29	0.00	-84.15	27.74	0.00
30	0.00	-83.60	28.28	0.00
31	0.00	-82.53	29.36	0.00

Appendix L. Justification for demographic parameter values employed in baseline VORTEX PVA model of Hainan gibbon population dynamics

Species description

Inbreeding

Small populations are vulnerable to genetic stochasticity, including inbreeding depression, loss of genetic diversity, and mutational accumulation (Frankham et al. 2009). To account for such genetic effects, inbreeding depression is incorporated into the VORTEX model as a reduction in first year survival among inbred individuals, a simplified but appropriate representation of the reduction in fitness that occurs in inbred populations (Lacy 1993). VORTEX uses the concept of 'lethal equivalents' to quantify the severity of the effect of inbreeding on juvenile survival. The number of lethal equivalents is the number of recessive lethal alleles per haploid genome that would cause the observed rate of inbreeding depression, and should not be confused with the inbreeding coefficient (F_{IS}, as discussed in Chapter 3), which indicates is the extent of inbreeding in the population. I opted to incorporate inbreeding into the baseline model as, although within my genetic analysis the direct assessment of F_{IS} did not shed light on the extent of inbreeding within the Hainan gibbon population, it did reveal a high level of relatedness between remaining individuals (see Chapter 3). This indicates that inbreeding is an issue for the population that should be incorporated into the population viability model.

The VORTEX programme uses a default value of 3.14 lethal equivalents per diploid genome to represent the effect of inbreeding on juvenile mortality. This value is a median mammalian value based upon a study of captive populations of 40 species by Ralls et al. (Ralls et al. 1988). Few quantitative data exist on the effect of inbreeding depression and number of lethal equivalents for individual species, but it appears that inbreeding effects extend to impacts upon lifetime survival rates and fecundity, and these effects are greater in wild populations (Crnokrak and Roff 1999). O'Grady et al. (2006) found an average overall effect of 12 diploid lethal equivalents across the demographic rates of wild population of 30 mammal and bird species. In one of the few cases where direct data is available for a primate species, the golden lion tamarin (*Leontopithecus rosalia*), the number of lethal equivalents was not quite as severe as this; found to be 5.0 (Brook et al. 2002). Furthermore, Frankham et al. (2014) recommend that for populations that have previously been subjected to bottlenecks (and thus have already purged highly deleterious alleles), a value lower than 12 but higher than 3.14 (which will underestimate the effect of inbreeding) is appropriate. For this reason, I specified a baseline value of 6 lethal equivalents but also tested the VORTEX default value of 3.14 lethal equivalents and 12 lethal equivalents (as per O'Grady et al. 2006) within the sensitivity analysis. I used the VORTEX default value of 50% for the percent of the total genetic load (i.e. lethal equivalents) that is due to recessive alleles, as this value is reportedly consistent with the data that exist for the few species that have been studied in this regard (Lacy 1993) and no alternative data appears to exist.

Reproductive parameters

Reproductive system

Long-term polygyny was specified as the reproductive system of the Hainan gibbon population. Behavioural observations of the population from multiple studies have pointed to a polygynous social structure within the Hainan gibbon social groups (Liu et al. 1987, Liu et al. 1989, Zhou et al. 2008b), and I observed two females within Group A simultaneously each carrying young during my own field work (pers. obs., June 2011). This goes against the traditional view that gibbons form long-term monogamous pairs, founded upon (predominantly) observations of non-crested gibbon, *Hylobates*, species (e.g. seminal work of Carpenter (1940) on *H. lar*). However, it appears that such a view may be obsolete, for crested gibbons at least, with several studies having reported polygynous groups (i.e. containing 2 or more adult females) of black crested gibbons, *Nomascus concolor* (Haimoff et al. 1986, 1987, Bleisch and Chen 1991, Jiang et al. 1999, Fan et al. 2006), and the Cao Vit gibbon, *Nomascus nasutus* (Geissmann et al. 2002, Chan et al. 2008, Fan et al. 2010), with at least one recent study confirming that such multi-female grouping can be maintained long-term (6 years) (Fan and Jiang 2010). Furthermore, if a 'short-term' model is selected VORTEX will randomly reshuffle mates every simulated year, which does not appear to occur in wild gibbon groups. Specifying long-term polygyny was the most accurate representation of the observed Hainan gibbon demography, as it permitted a model in which males were able to mate with more than one female at a time (as observed in wild population) but mate 'pairings' are maintained across years until the male or one of the females dies, when the pairings are reassigned – as occurs in wild gibbon populations (Palombit 1994, Chivers et al. 2013).

Age of first reproduction (i.e. at birth of first offspring)

VORTEX requires the median age at which individuals first produce offspring, rather than the age at which individuals become sexually mature as often, although an animal may be physically sexually mature, it will not have the ability or opportunity to produce offspring due to biological (e.g. gestation, body size) and ecological (e.g. competition) constraints. Hainan gibbons are reported to be sexually mature at around 5-8 years old (Chan et al. 2005), which is in line with other gibbon species, e.g. c. 6 years for *Hylobates lar* and *H. klossii* (Ellefson 1974, Tilson 1981), and 6-8 years for *Nomascus leucogenys* (Chivers et al. 2013) and *Hoolock hoolock* (Tilson 1979). Comparatively little data is available for the age at which gibbons first produce offspring, and no species-specific data exists reporting the age at birth of first offspring for the Hainan gibbon. Geissmann (1991) summarised the available data on captive gibbons, reporting an age at birth of first offspring ranging between c. 5 years to just over 9 years, with *N. leucogenys* ranging from 7.5-9 years. Compared to the age at sexual maturity for this species, this data supports a lag of 1-2 years after maturing before first offspring are produced, as expected. In the wild, it may feasibly be even later than this, given that nutrition and general quality of life is greatly enhanced in captivity. Gestation length is estimated to be 136–173 days (5.77 months) for the Hainan gibbon (Zhou et al. 2008b). Therefore we would expect the earliest potential age at birth of first offspring to be at least 6 years old, but the mean age is more likely to be closer to c. 8 years, or more. A value of 8 years for female age at first reproduction has been used in previous PVAs for other gibbon species (Tunhikorn et al. 1994, Traeholt et al. 2005).

The age at first reproduction for males has generally been assumed to be older, with these same PVAs for *H. lar, H. pileatus* and *N. gabriellae* (Tunhikorn et al. 1994, Traeholt et al. 2005) using a value of 10 years for males. In a PVA conducted for the closely related *N. nasutus*, Fan et al. (2013b) employed higher values of 10 years for females and 12 years for males, based upon field observations of *H. lar* by (Brockelman et al. 1998). Therefore, given the uncertainty surrounding this variable, I tested a range of values spanning the most likely values and those previously adopted for other gibbon species PVAs: females (8, 10) and males (8, 10, 12).

Maximum age of reproduction

This demographic variable is particularly difficult to measure, as it would require consistent monitoring of an individual gibbon's entire lifespan. Despite continued (but unfortunately discontinuous) monitoring of the population and extended field observations, the exact age of reproductive senescence and maximum breeding age of the Hainan gibbon are unclear. The reproductive period of the species has been estimated at 10-12 years (Li et al. 2010), although this may be an underestimate. If Hainan gibbons produce their first offspring at age 8 for females and 10 for males, and each sex has a reproductive lifespan of 10-12 years, then the age of reproductive senescence for the species could be as young as c. 20 years old. This is likely to represent the lower end of the scale however, and VORTEX uses the maximum breeding age observed to represent maximum age of reproduction.

The oldest known individual in the population ('B1'/'Lao Tai Tai') was estimated to be at least 43 years old in 2010 (Li et al. 2010). According to the accounts of the longest serving of

BNNR's field staff (Mr Chen Qing), who has been monitoring the gibbon population intermittently since 1984, 'B1' may have ceased breeding some time before 1998 as he observed her to no longer be breeding by around 1998-99 (Chen Qing, pers. comm., July 2011). If we assume 'B1' is presently 46 years old, and had ceased breeding by 1998, this would indicate reproductive senescence at around 31 years, and thus a likely maximum age of reproduction of approximately 30 years or younger. Previous gibbon PVA models (Tunhikorn et al. 1994, Traeholt et al. 2005, Fan et al. 2013b) have used an upper age limit for reproduction of 30 years, as representing a likely reasonable estimate of this value. I therefore, set the baseline value for this parameter to 30 years, but given the uncertainty surrounding this value, and its anticipated influence on the simulated population, I also tested additional values (26, 28, 32) to investigate the importance of this variable to the model outcomes.

Brood description (Maximum number of broods per year, maximum number of progeny per brood)

As previously stated, the gestation period of the Hainan gibbon is reported to be 136–173 days (5.77 months) (Zhou et al. 2008b). This is based upon a single observation. A similar, but slightly longer period has been reported for other gibbon species, e.g. 190-225 days for *H. lar*, and 200–212 days for *N. leucogenys* (Geissmann 1991) Allowing for lactational aenorrhea, it is very unlikely that a given female gibbon will produce more than one brood per year. The observed interbirth interval for gibbons (2-3 years, see discussion below) lends support to this value. Therefore, we can be fairly confident that the maximum number of broods per year is one.

All recorded Hainan gibbon births have consisted of one infant per female (Liu et al. 1984, Liu et al. 1989, Fellowes et al. 2008, Zhou et al. 2008b). Despite the reported ability of captive Siamangs (Dielentheis et al. 1991, Pra and Geissmann 1994), and wild white-handed gibbons (Ellefson 1974) to produce twins, multiple births in the Hylobatidae are exceptionally rare (Geissmann 1989b, Geissmann 1990), and I could find no record of an observation of a wild or captive *Nomascus* gibbon twin/multiple birth in the literature. Hainan gibbon females have never been observed to give birth to more than one infant at a time. It was assumed therefore that the Hainan gibbon has a maximum of one offspring per brood.

Sex ratio at birth (percentage of males)

Along with other mammals, the sex ratio at birth for gibbons is generally assumed to be equal i.e. the proportion of offspring born male is half or 50% (e.g. Tunhikorn et al. 1994). For the Hainan gibbon, there is some evidence that the ratio of offspring may be male-biased (Liu et al.

1989) (and see Chapter 2). It is difficult to ascertain if this ratio could be observed by chance alone but, as a skewed sex ratio may affect population growth through altered availability of mates, it was important to explore the influence of this factor upon the viability of the population. Therefore, I ran the baseline simulation using a proportion of 50% male offspring, as well as a sex ratio of three males to one female, i.e. 75% male offspring (sensitivity testing), as this is the ratio reported by Liu et al. (1989) and indicated by the genetic analysis conducted within this study. However, as both of these ratios (particularly the later) in fact correspond to the ratio of male to female offspring across all age categories (surviving beyond age one in Group B), rather than the exact ratio *at birth*, this may be an overestimate of the ratio and therefore any possible bias. Therefore, I also tested an additional intermediary value (65%) to assess a ratio of moderate bias.

Reproductive rate

Percentage of adult females breeding

The percentage of adult females breeding in a given year can be estimated from the observed interbirth interval (IBI) for the species. The IBI for the Hainan gibbon appears to be two years, with available data indicating births at a frequency of every two years (Liu et al. 1989, Chan et al. 2005, Fellowes et al. 2008, Zhou et al. 2008b). This corresponds to 50% of all adult females in the breeding pool breeding in a given year. The Hainan gibbon's IBI is slightly less than that reported for other gibbon species, with a period of around three years observed for many species, corresponding to 33% of females breeding, e.g. *Hoolock hoolock* (Molur et al. 2005) *Hylobates lar* (Tunhikorn et al. 1994), *H. klossii* (Tilson 1981), *H. agilis* (Mitani 1990) and *Nomascus annamensis* (Chivers et al. 2013).

The observed IBI of the Hainan gibbon is thought to coincide with the frequency of masting events of key food sources (*Litchi chinensis*, *Nephelium topengii*, and some *Ficus* spp.) which occur every two years (Zhou et al. 2008b). Alternatively, this shorter IBI may be a result of reduced interspecific competition for resources due to relatively low population density (c. 1.67 gibbons/km^2) within BNNR. Such flexibility in birthing interval may be possible; the observed IBI for *N. nasutus* in Vietnam also appears to be closer to two years (Ulrike Streicher pers. comm., September 2012), and the reported percentage of adult females breeding in a year for this species in China (30%) (Fan et al. 2013b) alludes to an IBI of around 2.8, while there is a single observation of an IBI of 17–22 months (c. 2 years) for *Nomascus gabriellae* (Chivers et al. 2013). For this reason, I set the baseline percentage of adult females breeding to 50% but also explored a value of 33% in sensitivity testing. No specific data are available on the amount of annual environmental variation in female reproductive success for the Hainan gibbon, but it seems likely such variation would be relatively low, so I set the standard deviation in the percentage of adult females breeding to 5%. To ascertain if Hainan gibbon population viability is sensitive to this particular variable, I also tested higher environmentally driven deviations as reported in previous gibbon PVAs (10%, 15%, 20%).

Mortality rate

Age-class specific mortality

Little information exists regarding Hainan gibbon mortality. No gibbon deaths were observed during the field seasons carried out within this study and no reports of any Hainan gibbon deaths were received from BNNR staff at any point during the study period or beyond. Accurate data on mortality rates requires intensive population monitoring, but monitoring of the Hainan gibbon has been episodic, meaning deaths may have occurred between monitoring sessions and so gone undetected. Detection of infant mortalities is particularly challenging, as even when consistently monitored, these individuals are less conspicuous. Furthermore, little is known about the fate of sub-adults after they disperse from their natal groups, as solitary individuals are exceptionally difficult to track and generally only encountered by chance. Over a seven year observation period Liu et al. (1989), recorded a 92% infant survival rate for the population, corresponding to a mortality rate of approximately 10%. No other mortality data for any other age class exists for the species, so it was necessary to look to the mortality rates reported for other gibbon species. Field data from the most closely related gibbon species, *N. nasutus*, indicates high mortality (20%) at age 0-1 (infants) and age 3-4 (small juveniles) (Fan et al. 2013b). This corresponds roughly to the pattern observed for most primates: high mortality in the post-natal period, which lowers following independence, and then peaks at the age at which maturing individuals migrate out of their natal group, followed by a gradual increase as the individual passes reproductive prime (Dunbar 1988). Traeholt et al. (2005) devised age-specific mortality rates for *Hylobates pileatus* and *Nomascus gabriellae* based upon thorough examination of the available data for gibbon mortality, which I adjusted for the Hainan gibbon.

Infant mortality was set to 10%, in line with Liu et al.'s (1989) observation. Traeholt et al. (2005) observed a mortality rate of 15% for dispersing gibbons. Dispersal age for Hainan gibbons appears to be at 7-8 years (Liu et al. 1989), as per other gibbon species, although individuals can be evicted from their natal group when as young as 5.5 years old (Zhou et al. 2008b). Available population data suggest that more dispersing sub-adults are leaving their natal groups than are forming new mating pairs (Liu et al. 1989), so it is possible that this life history stage could be the most critical for the species (Chan et al. 2005). No data exist on the exact rates of mortality for this age class, but assuming an IBI of two years, and an estimate of around 20 infants born in the last 10 years (from four breeding females in two social groups) with 80% surviving to pre-dispersal age, of these only around five solitary individuals have been observed as surviving dispersers. A further approximated 5 individuals of this age appear to remain in social groups, suggesting around 30% mortality at the age of dispersal. To be conservative, I set a level of 25% mortality for the dispersing age class (7-8 years), though it may be higher, to represent the elevated mortality at this age for this species. Mortality for all other age classes was set at 5%. I assumed that mortality rates were the same for both sexes in all age classes. To assess uncertainty regarding these estimates, and the influence of different levels of mortality upon the spices viability, I also explored additional values for the infant and dispersal age mortality rates (via sensitivity analysis). For the dispersal mortality I included an exceptionally high level (50%) given the concern surrounding this life stage. No data are available on the amount of annual variability in mortality due to environmental variation for any gibbon species, but this was assumed to be modest in the fairly stable BNNR environment. I arbitrarily set the standard deviation as 20% of the estimated level of mortality for each age class, as is likely in this suboptimal environment.

Mate monopolisation

Percentage of adult males breeding

The VORTEX system automatically assumes that mates are randomly reshuffled every simulated year, meaning that the percentage of adult males breeding can be used to specify whether any mate monopolization occurs. Deviations from 100% are generally engaged for species in which the established social structure results in the exclusion of a portion of adult males from the breeding pool. Existing observational data for gibbons indicate that all adult males are equally capable of mating (‘pairing’) with a female, given the opportunity (Molur et al. 2005). Therefore, although the Hainan gibbon is polygynous, all adult males in the population can be assumed (within the VORTEX model) to be available for breeding each year. As such the percentage of adult males in the breeding pool was set to 100%. To ascertain the influence of any exclusion of male mates, i.e. inaccuracies in this variable, I also tested additional values that represented decreasing degree of male reproductive success (90%-70%).

Carrying capacity

Within the PVA model the value of carrying capacity, ‘*K*’, serves to define an upper limit for the population supported by the given habitat, above which the population is truncated to *K*, so that the model can impose density-dependence on survival rates. If there were no ceiling on the growth possible, a situation representing infinite resources, the population would never be at risk of extinction, which is unrealistic for populations of threatened species. Resources are exceptionally limited for the Hainan gibbon population, with only a tiny 15 km^2 patch of suitable habitat within BNNR available to the population (Liu et al. 1989, Chan et al. 2005, Zhang et al. 2010). The carrying capacity of an available habitat is a difficult value to calculate for any population. Previous authors have used the approach of dividing the total habitat area available by the average exclusive home range for one gibbon group, and multiplying this by the average group size (Fan et al. 2013b). Using the estimate of available habitat (15 km^2), the exclusive home range estimate determined from my spatial analyses (1.43 km^2, corresponding to 95% of the average group home range of 1.5 km^2, see Chapter 2), and the average group size calculated from my field data (6.33 gibbons), yields an estimate of *K* equal to 65. However, this estimate is derived from observations of gibbons persisting in suboptimal conditions, meaning it may represent an overestimate of the actual carrying capacity of the BNNR landscape. The population has fluctuated between around 15 and 25 individuals for the last 30 years, but never increased to anything approaching a population of 65. Therefore, we can assume that the carrying capacity of the site is much lower.

To be conservative, I set a baseline *K* of 30. This value was necessary, as using a value for *K* any lower than 30 would have resulted in the VORTEX model constantly truncating the population to its initial size (25) and prohibited the simulation of the demographic processes. This also prevented the investigation (through sensitivity testing) of lower *K* values, which would be suggested by the previous, much larger estimates of the species home range size (Liu et al. 1989, Zhou et al. 2008b). I therefore tested a range of *K* values greater than 30 in case this estimate is too conservative and, more importantly, to reveal any sensitivity of the model to this attribute. (Further investigation of the sensitivity of the population's viability to available habitat was conducted in a specific scenario to explore this attribute). An upper value of *K*=80 allowed for an estimate in line with the home range requirements of the most closely related species, *Nomascus nasutus* (1.07 km^2; Fan et al. 2012). I did not incorporate any variability in the carrying capacity of the habitat due to environmental variation over time, as this variation was captured within the estimate of *K* derived from field data, which will have incorporated natural environmental variation.

Genetic management

VORTEX assumes that all animals in the initial population are unrelated. For the Hainan gibbon population we know that this is not true. The results of my genetic analyses (see Chapter 3) indicated that there was a generally high level of relatedness within one social group (as to be expected) but also between social groups. After 30 years at an exceptionally low population size, this is not surprising. I therefore chose for VORTEX to start the simulation with an initial population in which individuals were related in a manner specified by a pedigree file. When the details (age, sex, parents of each animal) of the initial population are specified in this manner, VORTEX begins the simulation using the individuals detailed in the pedigree, rather than using an assumed stable age distribution of randomly generated unrelated individuals. This pedigree was generated using the known relationships for the current population, based upon observations of the existing social groups and the results of my genetic analyses. This accounts for 36% of the current population. I assumed that all other individuals in the population (for which relationships were not known) were unrelated. This may mean I have still underestimated the degree of relatedness within the population, but including the pedigree of known relationships is still a better representation of the population and will more accurately capture the risk of population decline and extinction as a result of these relationships. I also specified a maximum number of two female mates to each male to imitate the observed reproductive system for the species (bigamy) and prevent males in the model from having more than 2 mates, which would overinflate the growth rate of the population. No sensitivity testing was required for these input variables.