Social structure and demography of a remnant Asian elephant *Elephas maximus* population and the implications for survival

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Abstract The Asian elephant *Elephas maximus* is at risk of extinction as a result of anthropogenic pressures, and remaining populations are often small and fragmented remnants, occupying a fraction of the species' former range. Once widely distributed across China, only a maximum of 245 elephants are estimated to survive across seven small populations. We assessed the Asian elephant population in Nangunhe National Nature Reserve in Lincang Prefecture, China, using camera traps during May–July 2017, to estimate the population size and structure of this genetically important population. Although detection probability was low (0.31), we estimated a total population size of c. 20 individuals, and an effective density of 0.39 elephants per km^2. Social structure indicated a strong sex ratio bias towards females, with only one adult male detected within the population. Most of the elephants associated as one herd but three adult females remained separate from the herd throughout the trapping period. These results highlight the fragility of remnant elephant populations such as Nangunhe and we suggest options such as a managed metapopulation approach for their continued survival in China and more widely.

Keywords camera trapping, demographic survival, *Elephas maximus*, habitat fragmentation, People's Republic of China, population thresholds, protected areas, Yunnan Province

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Introduction

Global elephant populations are declining. All surviving elephant species, the African bush elephant *Loxodonta africana*, African forest elephant *Loxodonta cyclotis* and Asian elephant *Elephas maximus*, are at risk of extinction as a result of habitat loss and fragmentation. These threats are further compounded by illegal poaching for ivory, meat and skin (Blanc, 2008; Choudhury et al., 2008). Once widespread across Asia, the Asian elephant is now the most threatened of the extant species, categorized as Endangered on the IUCN Red List (Choudhury et al., 2008). There are an estimated 41,000–52,000 animals in the wild, occurring in restricted populations in remaining range countries (Choudhury et al., 2008). Given the increased extinction risk posed by population restriction and fragmentation (Lacy, 2000; Frankham, 2005), especially for larger-bodied species (Hilbers et al., 2017), it is important to understand the demography of the remaining small populations so that effective management can be enacted.

Once widely distributed over southern China, only 221–245 elephants are now estimated to remain in Lincang, Pu'Er and Xishuangbanna Prefectures in southern Yunnan Province (Zhang et al., 2015). The population is fragmented into seven poorly connected subpopulations, with only four of these containing > 40 individuals (Zhang et al., 2015). Fragmentation has been driven by ongoing human population expansion, rapid land conversion to agriculture and expanding urbanization (Choudhury et al., 2008). Remnant populations are restricted to herds in small forest fragments within a human-dominated landscape (Choudhury et al., 2008). These small isolated populations probably suffer from genetic impoverishment and demographic stochasticity, leading to an increased risk of extinction (Lande, 1993; Frankham, 2003).

This study aims to determine the demographic and social structures of elephants in a remnant population in Nangunhe National Nature Reserve, Lincang Prefecture, situated at the border between China and Myanmar. Previous studies of elephants in Nangunhe have focused

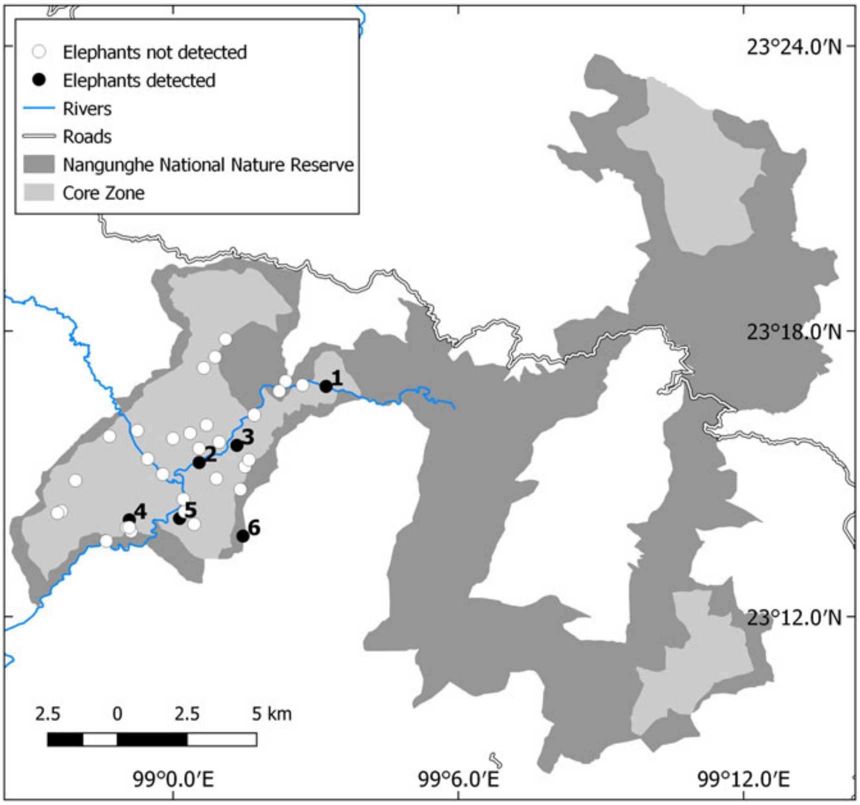

FIG. 1 Positions of camera traps within the Cangyuan section (core zone) of Nangunhe National Nature Reserve, south of Lincang Prefecture, China. The six cameras at which elephants were detected are numbered (see text for details).

on either habitat associations (Feng et al., 2010) or were part of national assessments of population size (e.g. Zhang et al., 2015). The elephant population in Nangunhe is regarded as genetically distinct, despite a small estimated population size of 20–23 individuals in 2014, with the highest nucleotide and mitochondrial haplotype diversity of China's elephant populations (Zhang et al., 2015). The importance of the Nangunhe population for elephant conservation in China, and the region more generally, is therefore potentially significant. Here, we aim to provide insights that could improve conservation of Asian elephants, offering support for a metapopulation management approach.

Study area

Nangunhe National Nature Reserve is a 708 km² national protected area located in the south of Lincang Prefecture (Bohnett et al., 2015). It lies within the south-west monsoon climate zone and supports bamboo forest, monsoon evergreen broadleaved forest, seasonal rainforest, shrubland and tall grassland (Liu et al., 2016). The reserve includes an 85.3 km² core zone, 89.4 km² buffer zone and 101.8 km² experimental zone within Cangyuan county, with the remaining 431.5 km² in Gengma county. Elephants are restricted to the section of the reserve in Cangyuan county, predominantly utilizing the core zone in the west (Fig. 1), which experiences minimal human disturbance (Yunnan Forestry Administration, unpubl. data). The reserve is isolated from other forested protected areas supporting elephant populations in China as the human-dominated landscape prevents elephant movement between fragments.

Methods

A total of 36 motion-triggered camera traps (26 Onick AM-999, Wuhan, China; eight Ltl Acorn 6210, Shenzhen, China; two ScoutGuard SG560 K, Molendinar, Australia), with infra-red illumination, were placed over a 44 km² area within the core zone of the reserve to determine elephant population size, density and social structure (Fig. 1). The cameras were active for 47 days during May–July 2017 (the rainy season), although not all cameras were continually operational over the entire period, giving 1,394 trap days. The reserve manager advised that elephants predominantly use the core zone because the surrounding buffer and experimental zones contain steep slopes, farmlands, roads and settlements. To maximize detectability, cameras were installed along known elephant trails at c. 1-km intervals, across all vegetation types. Cameras were set at a height of 1.5 m, at a focal distance of c. 5 m (Varma et al., 2006). Cameras were directed either north or south to avoid sun glare and any overhanging vegetation was cleared to prevent false triggers. One camera was set per station, which were set in positions where the angle of view was along trails, with little potential for movement outside the camera's field of view. Cameras were configured to take three photographs and 10 seconds of video per trigger, although malfunctions caused eight cameras to take exclusively either photographs or video, and two cameras took a 3 second video only.

Individuals were identified, aged and sexed using distinguishing traits, and ages of non-adults were estimated by comparing animal heights relative to an adult female where they co-occurred in the same photograph (de Silva et al., 2011; Vidya et al., 2014). Individuals were grouped into four age classes: calf (≤ 6 months), infant (7 months–2 years), juvenile (3–7 years) and adult (≥ 8 years). The adult age class incorporated subadults, as distinguishing between adults and subadults based on relative height measurements is unreliable. All juveniles and adults were assigned a sex, but calves and infants were left unsexed as these age classes lack discriminating sexually dimorphic features (Varma et al., 2012).

Population size was estimated using Chao's moment estimator (*M*th model) in *CAPTURE* (Hines, 1987), which accounted for the effects of time (t) and individual differences (h) (Seltmann et al., 2018). A closure test was applied to ensure the population met the assumption of a closed population.

Capture probabilities across the survey area, and elephant density, were assessed using a spatially explicit capture–recapture model with the package *secr* (Efford, 2018) implemented in *R 3.4.1* (R Core Team, 2017). The spatial scale of capture location data (σ) was estimated to be 1.8 km, as a proxy of elephant home range size in the reserve, calculated as the mean maximum distance moved. The initial *secr* buffer width was taken as 2σ (3.6 km), which was adequate for density estimates to stabilize across the camera grid.

Social structure was determined by assigning individuals to the same group if they were captured within 15 minutes of each other (Head et al., 2013). Any residual individuals were considered part of a group if they were captured with one or more of its members. Individual elephants captured more than 30 minutes apart on the same camera were considered to be independent capture events.

Results

Camera trapping in Nangunhe National Nature Reserve yielded a total of 154 images and 43 videos of elephants on six of the 36 camera traps, of which 89 images (58%) and 37 videos (86%) were suitable for elephants to be individually identified, sexed and assigned an age class. Sixteen elephants were individually identified: eight adult females, one adult male, three juvenile males, and two infants and two calves of indeterminate sex (Supplementary Table 1). Using Chao's *M*th model, the total population size in the reserve was estimated to be 20 individuals (95% CI 17–33). The spatially-explicit likelihood capture model estimated the detection probability ($g0$) to be 0.31 (95% CI 0.26–0.37) over the trapping grid, with an elephant density of 0.39 individuals per km^2 (95% CI 0.14–0.67 individuals per km^2).

Of the 16 elephants identified, 11 formed one herd (Supplementary Table 2), although not all members were captured together on every occasion (Supplementary Table 3). Females F04 and F06, juveniles J01 and J03, and calves C04 and C06 were recorded together in four capture events on camera traps 2 and 3. Female F05, juvenile J02 and calf C05 were absent from one capture event. Adult female F07 was captured only once in the presence of a recognized herd member (juvenile male J02), although there was a 22-minute separation, and more than an hour after the rest of the herd was captured on the same camera trap. An adult female (F02) was captured once with her calf (C02) on camera trap 5 (Fig. 1). Three solitary adult females (F01, F03 and F08) were detected, with F03 and F08 captured once on camera traps 1 and 2, respectively, and F01 captured in seven separate events on camera traps 3, 4, 5 and 6 (Fig. 1). Only one adult male (M01) was encountered, detected on his own three times on camera trap 2, and once with the herd on camera trap 3, although one capture on camera 2, on 29 May, was only 24 minutes after the other herd members.

Discussion

We estimate that the elephant population of Nangunhe National Nature Reserve is 20 individuals, with an estimated density of 0.39 elephants per km^2. This density is relatively low compared to densities of 3.3 elephants per km^2 in Nalkeri Reserve Forest, India (Karanth & Sunquist, 1992), and 5.0 elephants per km^2 in Bandipur National Park, India (Johnsingh, 1983), although densities can be < 0.1 per km^2 (Sukumar, 1989). The area of suitable habitat for elephants in Nangunhe covers only 29 km^2 of the Reserve (Liu et al., 2016), which is less than the estimated minimum species' home range size of 100 km^2 (Jathanna et al., 2015; Liu et al., 2016), potentially limiting the carrying capacity of the Reserve (Zhang et al., 2015).

The elephant population in Nangunhe has not increased for more than 4 decades, which equates to approximately two generations (Choudhury et al., 2008). The size of the population has reportedly fluctuated around 20 individuals since 1976, with the exception of a decline to 12 individuals in 1983 (Zhang et al., 2015). Although apparently stable over this period, the population remains vulnerable to accelerated inbreeding and loss of genetic diversity leading to inbreeding depression and a compromised ability to respond to changing environmental conditions (Frankham, 2003, 2005). This is compounded by demographic and environmental stochasticity and local catastrophes that together lead to an increased risk of population extinction

(Lande, 1993). From the data collected we determined there to be at least eight adult females, although their ages and reproductive status cannot be determined using our methods. There were seven young animals, at least four of which (two infants and two calves) were assumed to be dependents. Asian elephants are known to experience senescence, with reproductive success declining beyond the age of 18 years (Hayward et al., 2014). The age of first reproduction for females is 6–9 years and the average interbirth interval is 2.5–4 years (Sukumar, 2003). Without further details of female ages it is not possible to predict future demographic trends.

However, the detection of only one adult male in Nangunhe suggests a reduced effective population size, exacerbating the risks of inbreeding and reducing the long-term sustainability of the population (Frankham, 2005; Allendorf et al., 2008). The observed adult sex ratio of the population was female-biased (1:8). It is possible that the number of males was underestimated, particularly if they range more widely than females (Sukumar, 1989). We also acknowledge the low detection rate indicated by capture models, which could have resulted in individuals not being detected. Anecdotally, the reserve manager reported knowledge of only two adult males in the Nangunhe population over the last 5 years (Li, pers. comm.). This suggests a strong female-biased adult sex ratio, seldom seen in undisturbed populations, which tend to exhibit adult sex ratios of 1 adult male:2 adult females (Gupta et al., 2016). The underlying reasons for the skewed sex ratio in Nangunhe are unclear. There are recorded incidences of poaching of adult male elephants in Nangunhe, although not in the last 14 years. Of eight animal deaths reported during 1987–2003, one adult male was killed in retaliation for eating crops in 1996 and another was poached for ivory in 2003 (Liu et al., 2016). The sex of other animals killed was not recorded.

Assessments of sex ratios at birth, or examination of differential survival and mortality rates in younger animals, are thwarted by our inability to distinguish the sex of calves or infant elephants. Theories exist to explain sex ratio biases at birth and the effect of maternal (Trivers & Willard, 1973; Rosenfeld & Roberts, 2004) or paternal (Malo et al., 2019) conditions that may have relevance given the largely suboptimal habitat of Nangunhe and potential levels of inbreeding.

An important consideration is that elephants are highly complex social animals, and it is likely their breeding biology is similarly complex. For example, Asian elephants do not breed well in captivity (Taylor & Poole, 1998; Rees 2003; Wiese & Willis, 2004), where groups are structured artificially. In response to severely reduced population size, the elephant population in Cat Tien National Park, Viet Nam, coalesced into a single group comprising many matrilines (Vidya et al., 2007). The impact of historical hunting, which is often highly selective, may affect population demography by removing key individuals such as experienced females or reproductively successful males and altering social relationships (Archie & Chiyo, 2012) and, in African elephants, can result in a bias towards adult females (Jones et al., 2018). Prior to the recorded poaching in Nangunhe, the population will have been subject to the same pressures that have caused the decline of elephants across China more widely (Elvin, 2006). As a consequence, the structure of the Nangunhe population, probably like many other small populations, is an artefact of human activity rather than natural processes and therefore, in common with captive groups, the requisite social processes required to facilitate breeding in this complex species may be lacking.

The identified presence of lone female elephants in Nangunhe corresponds with similar findings reported by Fernando & Lande (2000) who identified female Asian elephants in Ruhuna National Park, Sri Lanka, which spent considerable time away from their natal herds to maximize foraging opportunities. The low male to female ratio amongst adult elephants could also influence the dispersal of females. In elephants males typically seek mates, but in African elephants a lack of mating opportunities has also been found to increase female dispersal rates (Archie et al., 2007).

The picture developing for elephants in Nangunhe, from our study and others, suggests a remnant population that is at risk of being lost because of social, genetic, ecological and human factors resulting from its isolation. The spatial and temporal scales that are relevant for elephant conservation create further problems. The long generation length (20–25 years) of Asian elephants (Choudhury et al., 2008) means that any detrimental effects of inbreeding may take a substantial period of time to manifest in the population (Ling et al., 2016), but is likely to present a long-term problem for the elephants of Nangunhe unless gene flow is restored between unrelated populations. The addition of only one breeding immigrant could substantially reduce inbreeding depression in an inbred population (Vilà et al., 2003). However, there are no current natural migratory routes between Nangunhe and the six other elephant populations in China. Corridors for elephants have been successfully created elsewhere (Green et al., 2018), but can require substantial land-use changes and agreement from stakeholders in the interstitial areas between reserves. Efforts to develop transboundary corridors linking Nangunhe to potentially large areas of suitable habitat (Leimgruber et al., 2003) and elephant populations in Myanmar would probably be complicated. Remaining options include translocations between elephant populations within China (Ishida et al., 2018), or assisted reproductive technologies to restore gene flow (Hermes et al., 2013), each requiring significant investment of effort and resources.

We suggest that the continued existence of elephants in Nangunhe, and the six other remaining populations in China, requires a wider landscape and metapopulation approach to species management, which has been shown to work elsewhere (e.g. Flagstad et al., 2012). This should be conducted in concert with continued information gathering about the status of these populations, perhaps taking advantage of increasingly accessible technologies. To enact a sufficiently robust and adaptive collective management approach to these populations, more detailed information about social structures and relatedness will be required.

As throughout much of Asia, rural communities surrounding Nangunhe are dependent on agriculture, potentially exacerbating conflict, as seen in other areas where ranges of elephants and people overlap significantly (Fernando et al., 2019). As in China, protected areas elsewhere are rarely sufficient to maintain viable populations of Asian elephants (Fernando et al., 2006), making their long-term survival dependent on suitability of surrounding wildlands (Leimgruber et al., 2003) and perhaps less optimal habitats (Evans et al., 2018). Efforts to address issues of habitat and human disturbance within and around reserves should be maintained or enhanced. But it is only by considering these fragmented populations as a single entity, with appropriate linking management, perhaps akin to a breeding programme, that we can hope to ensure the long-term survival of Asian elephants in China and the wider region.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. All research was approved by Marwell Wildlife's Ethics Committee and the ethical review processes of the University of Southampton and Beijing Forestry University.

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