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 is at risk of extinction due to 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 between May to July 2017, to estimate the population size and structure of this genetically important population. Our results indicate that whilst detection probability was low (0.31), we estimated a total population size of approximately 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

Habitat fragmentation, population thresholds, demographic survival, camera trapping, protected areas, People's Republic of China, Yunnan Province.

Introduction

Global elephant populations are declining. All surviving elephant species, the African bush elephant (*Loxodonta africana*), African forest elephant (*L. cyclotis*) and Asian elephant (*Elephas maximus*) are currently at risk of extinction due to 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 among the extant species, listed as Endangered by the IUCN Red List of Threatened Species (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 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 sub-populations, with only four of these containing more than 40 individuals (Zhang *et al*., 2015). Fragmentation has been driven by ongoing human population expansion, rapid land conversion to agriculture and expanding urbanisation (Choudhury *et al*., 2008). Remnant populations are restricted to 'pocketed herds' in small forest fragments within a human-dominated landscape (Choudhury *et al*., 2008). These small isolated populations are likely to suffer from genetic impoverishment and demographic stochasticity leading to an increased risk of extinction (Frankham, 2003; Lande, 1993).

This study aims to determine the demographic and social structures of elephants in a remnant population in Nangunhe National Nature Reserve (南滚河国家级自然保护区), Lincang Prefecture, situated on the border between China and Myanmar. Previous studies of elephants in Nangunhe have focused on either habitat associations (Feng *et al*., 2010) or as 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 population size estimated at 20-23 individuals in 2014, with the highest nucleotide and mitochondrial haplotype diversity of all 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 important insights that might improve conservation of Asian elephants, offering support for a metapopulation management approach.

Study area

Nangunhe National Nature Reserve is a 708 km^2 national protected area located in the south of Lincang Prefecture (Bohnett *et al*., 2015). It lies within the southwest 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 km^2 core zone, 89.4 km^2 buffer zone and 101.8 km^2 experimental zone within Cangyuan county, with the remaining 431.5 km^2 in Gengma county. Elephants are restricted to the section of the reserve in Cangyuan county, predominantly utilising the core zone in the west (fig. 1), which experiences minimal human disturbance (Yunnan Forestry Administration, unpublished 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 active motion-triggered camera traps (26 Onick AM-999, eight Ltl Acorn 6210 and two ScoutGuard SG560K), with infra-red illumination, were placed over a 44 km^2 area within the core zone of the reserve (23°14'38" N 99°00'24" E) to determine elephant population size, density and social structure (fig. 1). The cameras were active for 47 days between May and 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 as the surrounding buffer and experimental zones contain steep slopes, farmlands, roads and settlements. To maximise detectability, cameras were installed along recorded elephant trails at approximately 1.0 km intervals, across all vegetation types. Cameras were set at a height of 1.5m, at a focal distance of approximately 5m (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 angle of view was along trails, with little potential for movement outside of 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 three 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 (Silva *et al.*, 2011; Vidya *et al.*, 2014). Individuals were grouped into four age classes: new-born (≤ 6 months), infant (7 months-2 years), juvenile (3-7 years) and adult (≥ 8 years). The adult age class incorporated sub-adults, as distinguishing between adults and sub-adults based on relative height measurements is unreliable. All juveniles and adults were assigned a sex, but new-borns and infants were left unsexed as these age classes lack the discriminating sexually dimorphic features (Varma *et al.*, 2012).

Population size was estimated using Chao's moment estimator (M*th* model) in programme 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 that 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 in the package *secr* implemented in R (Efford, 2018). 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 (MMDM). 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 NNR 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; two infants and two new-borns, both pairs of indeterminate sex (Table S1). Using Chao's *Mth* model, the total population size in the reserve was estimated to be 20 individuals, with 95% confidence intervals between 17 and 33 animals. The spatially-explicit likelihood capture model estimated the detection probability (g_0) to be 0.31 (95% CI: 0.26 - 0.37 km^{-2}) over the trapping grid, with an elephant density of 0.39 animals km^{-2} (95% CI: 0.14 - 0.67 animals km^{-2}).

Of the 16 elephants identified, 11 formed one herd (Table S2), although not all members were captured together on every occasion (Table S3). 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 29th May, was only 24 minutes after the other herd members.

Discussion

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

The elephant population in Nangunhe has not increased for more than four 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 new-borns) 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 between six and nine years and the average interbirth interval is between 2.5 to four 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 (Allendorf *et al*., 2008; Frankham, 2005). 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 might result in missed individuals. Anecdotally, the reserve manager reported knowledge of only two adult

males in the Nangunhe population over the last five years (Li *pers.comm*.). This suggests a strong female-biased adult sex-ratio, seldom seen in undisturbed populations that tend to exhibit adult sex ratios in the region of 1 adult male: 2 adult females (Gupta *et al*., 2016). The underlying reasons for the sex ratio skew in Nangunhe are unclear. There are recorded incidences of poaching of adult male elephants in Nangunhe, though not in the last 14 years. Of eight animal deaths reported between 1987 and 2003, one adult male was killed in retaliation for crop-raiding 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 new-born or infant elephants. Theories exist to explain sex-ratio biases at birth and the effect of maternal (Rosenfeld & Roberts, 2004; Trivers & Willard, 1973) or paternal (Malo *et al.*, in press) conditions which may have relevance given the largely sub-optimal habitat of Nangunhe and potential levels of inbreeding.

An important consideration is that elephants are highly complex social animals, and it is highly probable that their breeding biology is in turn similarly complex. For example, Asian elephants do not breed well in captivity (Wiese & Willis 2004; Rees 2003; Taylor & Poole 1998), where groups are structured artificially. In response to severely reduced population size, the elephant population in Cat Tien National Park, Vietnam, coalesced into a single group, comprised of 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 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 highly 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 that spent considerable time away from their natal herds to maximize foraging opportunities. The low male to female ratio amongst adult elephants might also influence the dispersal of females. In elephants, males typically seek mates, however 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 ours and other studies, suggests a remnant population that is at risk of being lost due to social, genetic, ecological and human factors resulting from its isolation. The spatial and temporal scales that are relevant for elephant conservation efforts 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 might 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), though 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 likely prove even more 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 investments 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. Indeed, 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 NGH 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 are rarely sufficient to maintain viable populations of Asian elephants (Fernando *et al.*, 2006), making their long-term survival dependant 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, and indeed 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 region.

Author Contributions

LJH designed the project, carried out fieldwork, collected field data, analysed data, wrote and edited manuscript text. KS designed the project, facilitated fieldwork, wrote and edited manuscript text. TCG analysed data, wrote and edited manuscript text, KSHP designed the project, wrote and edited manuscript text, PR designed the project, analysed data, wrote and edited manuscript text.

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Conflicts of Interest

None

Ethical Standards

This work complies with the journal's Code of Conduct. All work was cleared by Marwell Wildlife's Ethics Committee and the ethical review processes of the University of Southampton and Beijing Forestry University.

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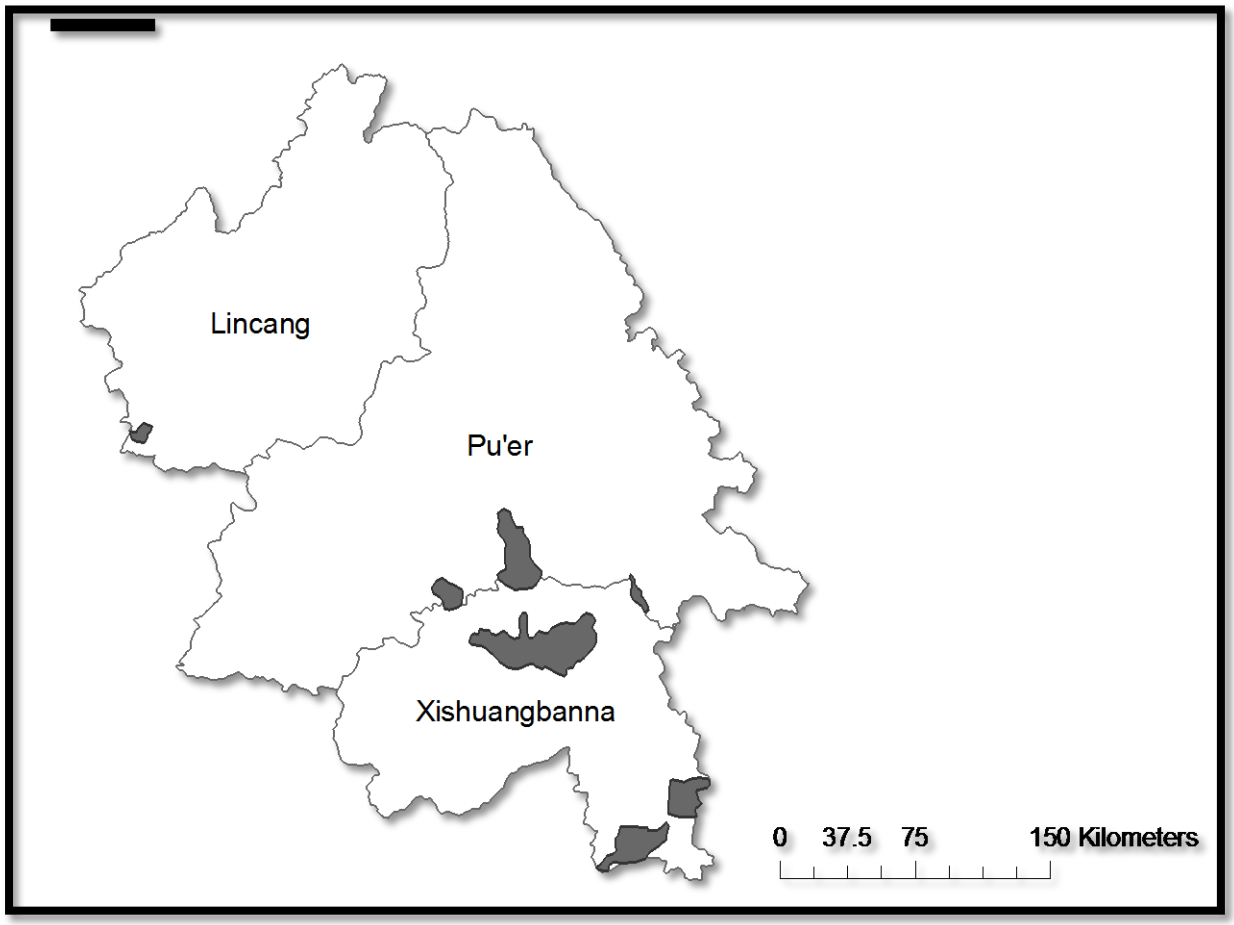
440 **Fig. 1**



441

Hale *et al*. Social structure and demography of a remnant Asian elephant (*Elephas maximus*) population and the implications for survival

Supplementary Materials

Table S1. Sex and ages classes of individual elephants encountered on camera traps in Nangunhe National Nature Reserve.

Elephant ID	Sex	Age class
C02	Unknown	Infant
C04	Unknown	Infant
C05	Unknown	New born
C06	Unknown	New born
F01	Female	Adult
F02	Female	Adult
F03	Female	Adult
F04	Female	Adult
F05	Female	Adult
F06	Female	Adult
F07	Female	Adult
F08	Female	Adult
J01	Male	Juvenile
J02	Male	Juvenile
J03	Male	Juvenile
M01	Male	Adult

453 Table S2. Encounter matrix between elephants in Nangunhe National Nature Reserve, showing
454 the number of occasions on which individuals were captured on camera trap images within 15
455 minutes of each other (after Head et al, 2013 – see Methods in main text).

456

	C02	C04	C05	C06	F01	F02	F03	F04	F05	F06	F07	F08	J01	J02	J03	M01
C02	-															
C04		-														
C05			-													
C06		4	2	-												
F01					-											
F02	1					-										
F03							-									
F04		4	2	4				-								
F05		3	2	3					-							
F06		4	2	4				3	2	-						
F07											-					
F08												-				
J01		4	2	4				4	3	4			-			
J02		3	2	3				3	2	3			3	-		
J03		4	2	4				4	3	4			4	3	-	
M01		1	1	1				1	1	1			1	1	1	-

457

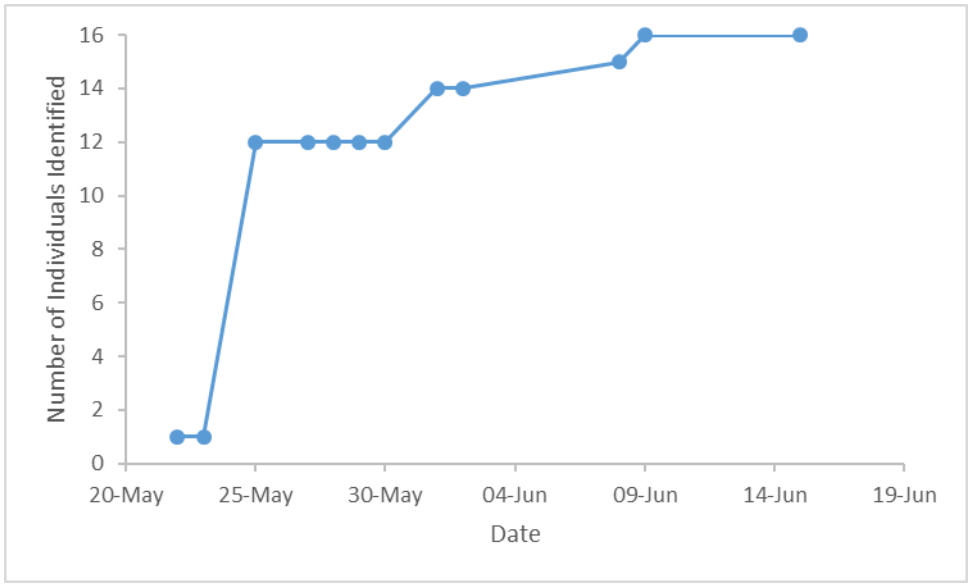
458 Table S3. Individual elephant camera trapping capture histories in Nangunhe National Nature
459 Reserve, by date and camera ID. Elephant IDs indicate sex of adults ("M" or "F" prefixes
460 referring to males and females respectively), with juveniles and calves denoted with "J" and "C"
461 prefixes respectively.

462

	May						June					
Date:	**22**	**25**	**28**	**29**	**30**	**31**	**02**	**03**	**08**	**09**	**15**	**Total**

Camera ID:	5	1	3	6	2	5	2	2	6	5	4	2	2	3	
Elephant ID															
C02										1					1
C04			1				1	1				1			4
C05			1									1			2
C06			1				1	1				1			4
F01	1			1		1			2		1			1	7
F02										1					1
F03		1													1
F04			1				1	1				1	1		5
F05			1					1				1			3
F06			1				1	1				1	1		5
F07												1			1
F08													1		1
J01			1				1	1				1			4
J02			1				1	1				1			4
J03			1				1	1				1			4
M01			1		1		1	1							4
Total	**1**	**1**	**10**	**1**	**1**	**1**	**8**	**9**	**2**	**2**	**1**	**10**	**3**	**1**	**51**

Figure S1. Accumulation curve for number of individual elephants encountered in Nangunhe National Nature Reserve during camera trapping during May and June 2017.


Number of Individuals Identified
16
14
12
10
8
6
4
2
0
20-May
25-May
30-May
04-Jun
09-Jun
14-Jun
19-Jun
Date

469

470