DOI: 10.1002/inc3.10

RESEARCH ARTICLE



Check for updates

China's wandering elephants: Integrating exceptional movements into conservation planning

Ahimsa Campos-Arceiz¹ | J. Antonio de la Torre^{1,2} | Ke Wei³ | Xiaoyu O. Wu⁴ | Yang Zhang¹ | Yufei Zhu¹ | Zicheng Yang⁵ | Shu Chen⁶ | Yang Bai⁷ | Richard T. Corlett⁷ | Fei Chen⁵

¹Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences & Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, China

²Programa Jaguares de la Selva Maya/Bioconciencia A.C. Ocotepec L10 Mz 74, San Jeronimo, La Magdalena Contreras, Mexico City, Mexico

³Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, China

⁴School of Engineering and Building Environment, Griffith University, Nathan, Queensland, Australia

⁵Asian Elephant Research Center of National Forestry and Grassland Administration, Southwest Survey and Planning Institute of National Forestry and Grassland Administration, Kunming, China

⁶Zoological Society of London, Regent's Park, London, UK

⁷Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, China

Correspondence

Ahimsa Campos-Arceiz, Megafauna Ecology and Conservation Group, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China. Email: ahimsa@xtbg.ac.cn

Fei Chen, Asian Elephant Research Center of National Forestry and Grassland Administration, Southwest Survey and Planning Institute of National Forestry and Grassland Administration, Kunming 650031, China. Email: flying87@vip.qq.com

Funding information

Southeast Asia Biodiversity Research Institute, Grant/Award Number: Y4ZK111B01

Abstract

In May-June 2021 a herd of wild Asian elephants made global headlines when they trekked hundreds of km into areas where elephants had been absent for centuries, mobilizing a response of unprecedented scale. Here, we analyze the movement attributes and body condition of these elephants to understand this unusual behavior and its implications for megafauna conservation in the Anthropocene. We propose that these movements are a form of partial and irruptive nomadic behavior, although the data is also compatible with a failed attempt of dispersal. In their path to Kunming, the elephants made unusual habitat choices, using landscapes with higher nightlight intensity, and moving close to towns and villages, while avoiding areas with high forest cover, which we interpret as habituation to feeding on crops and lack of fear of people. Fifteen months after starting their journey, the elephants showed high body condition scores and had successfully delivered two babies, both indicators of good health, suggesting that their decision to leave their previous home range had paid off. In China, we recommend an elephant conservation strategy founded on area-based and area-specific measures, including protected areas, landscape connectivity, and the mitigation of human-elephant conflicts, as well as preparedness for expectable population range expansions, potentially on the scale of hundreds of km, in the coming decades. Our study highlights the ecological and behavioral plasticity of elephants and the importance of integrating movement ecology in conservation planning, especially for wide-ranging species.

KEYWORDS

Asian elephant, dispersal, Elephas maximus, migration, nomadism, sedentarism

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. Integrative Conservation published by John Wiley & Sons Australia, Ltd on behalf of Xishuangbanna Tropical Botanical Garden (XTBG).

1

1 | INTRODUCTION

Human alteration of ecosystems has caused a global disruption of animal movements, with potential knock-on effects on populations, communities, and ecosystem function (Tucker et al., 2018). Habitat loss, fragmentation, barrier effects, and changes in resource distribution alter the way animals move (Shepard et al., 2008), particularly wide-ranging species, and these alterations will increase with climate change (e.g., Seebacher & Post, 2015). Given the impact of movement on animal survival and reproductive success (Morales et al., 2010), understanding the movement ecology of threatened species is important for the design of effective conservation strategies (Allen & Singh, 2016).

There are four broadly recognized animal movement types: sedentarism, migration, nomadism, and dispersal (see Glossary and Supporting Information: Figure S1; Allen & Singh, 2016; Bunnefeld et al., 2011; Mueller & Fagan, 2008; Roshier & Reid, 2003; Teitelbaum & Mueller, 2019). Knowing whether a population is sedentary (i.e., animals occupy stable home ranges), migratory, or nomadic, and whether it has propensity for dispersal, is important to determine the conservation actions needed to protect it. For example, a network of protected areas may be most suitable to conserve sedentary animals, while time-specific measures might be more cost-effective to conserve migratory or nomadic animals that only spend part of the year in a landscape. Furthermore, understanding finer-scale movement characteristics is key for finer-scale planning, design, and implementation. For example, knowing home range sizes, habitat preferences, dispersal distances, the location of seasonal ranges, or the timing and scale of migrations is key to design the size and location of protected areas, priority habitats to restore, or the appropriate timing of time-specific measures (Allen & Singh, 2016).

As the largest terrestrial animals, elephants are the quintessential wide-ranging animals whose movements are compromised in the Anthropocene (Leimgruber & Songer, 2021). Female elephants live in family groups with their dependent offspring, while males live solitarily or in loose social associations after dispersing from their natal groups (Charif et al., 2005; de Silva et al., 2011). Elephants are generally sedentary, with welldefined home ranges (e.g., Wall et al., 2021). African savanna elephants (Loxodonta africana), however, are partial and facultative migrators, with a small proportion of individuals in many populations undergoing annual migrations, although not every year, in response to seasonal changes in rainfall (Purdon et al., 2018). Despite much speculation and discussion about migration and migratory routes (e.g., Choudhury, 1999; Davidar et al., 2012; Koirala et al., 2016; H. Wang et al., 2021), there is no evidence of migratory movements among Asian

elephants (*Elephas maximus*; Fernando et al., 2008). Natal dispersal among elephants is done by males at adolescence, while females are assumed to have permanent home ranges where they spend their whole lives (Vidya & Sukumar, 2005). There are, however, exceptional circumstances under which female herds may disperse and shift their home ranges, for example, when a herd becomes too big and splits in two, or when a drastic environmental change renders their home range unsuitable (Sukumar, 2003).

In May-June 2021, a group of Asian elephants in Southwest China made global headlines when they trekked into areas where elephants had been absent for centuries, eventually reaching the outskirts of Kunming, the capital city of Yunnan. The group had left its former home range in the Mengyang section of the Xishuangbanna National Nature Reserve (hereafter Mengyang; 22.2°N, 100.9°E) 1 year earlier, in March 2020, simultaneously with a second herd that walked southward but received much less international attention (Campos-Arceiz et al., 2021).

Much has been discussed about the causes of (Campos-Arceiz such behavior. Elsewhere et al., 2021), we argued that both elephant herds moved away from their home ranges in Mengyang because of resource limitation caused by the interaction of three processes: (1) the ongoing growth of the local elephant population (e.g., Liu et al., 2017; Zhang et al., 2015), (2) the thickening of the forest canopy within the Nature Reserve, which reduces the availability of elephants preferred food plants (K. F. Yang et al., 2018), and (3) an extreme drought that hit Yunnan from March 2019 to March 2020 (H. Wang et al., 2021). Elephant herds moving away from their traditional home ranges in Mengyang is not a new phenomenon. At least nine elephant dispersal events have been recorded in the area since the 1990s, in which elephant herds abandoned their original home ranges and established in neighboring areas (Figure 1). Expansive range shifts are expectable in a population that is growing and geographically expanding, as is the case in China. More puzzling was the behavior of the group that moved hundreds of km outside of the population range and into an 8.4-millionperson city. What kind of behavior explains such long-distance movements into unfamiliar areas, what were the consequences of such behavior for the elephants, and what lessons can be learned for conservation?

This unusual, well-documented, and high-profile elephant behavior presents an opportunity to investigate the consequences of global environmental change for the movements of very large, mobile, and conflict-prone wildlife. Here, we analyze the movement attributes and the body condition of the herd that walked to Kunming to shed light on this behavior and its implications for conservation. First, we analyze their movement type to test whether it

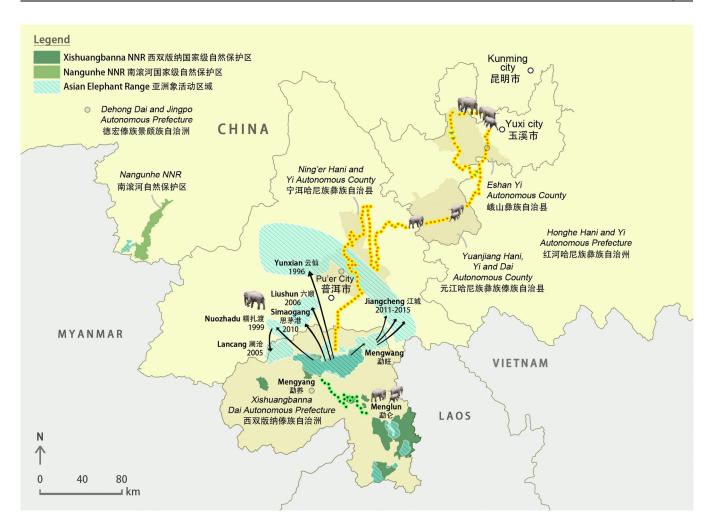


FIGURE 1 Movement paths of the two elephant herds that left Mengyang in March 2020. The yellow dotted line represents the movements of the Kunming herd, while the green dotted line represents the XTBG herd. Black arrows indicate recent dispersal events, in which elephant herds shifted their home ranges; years indicate the time of the dispersal event. Please note that some herds shifted range more than once. See Supporting Information: Appendix S1 for a detailed chronology.

should be considered a migration (as often suggested), dispersal, or something else; second, we investigate aspects of their movement characteristics, specifically the effect of landscape features on their habitat use and selection along their path; and third, we assess their body condition as a way to evaluate the health outcome of 15 months moving outside their traditional home range. We then discuss the current and future conservation implications of this behavior, particularly in the context of the new National Park that the Chinese authorities are currently designing for elephant conservation in Southwest China (e.g., S. Chen et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Chronology of the elephant movements

Figure 1 and Supporting Information: Figure S2 and Appendix S1 provide a detailed chronology of the movements of the Kunming herd between March 2020 and October 2021. On 2nd June 2021, when the elephants entered the outskirts of Kunming, showing no signs of changing direction, a decision was made to influence their movements (by means of food lures and path blocks) to guide them back toward the south. From this moment, the authorities had a strong influence on the direction and path of the elephants' movements. By mid-September 2021, the Kunming herd was back within recent elephant range and in October 2021 they had returned to their estimated former range in Mengyang. The other herd (known as XTBG herd) returned to Mengyang in August 2021, also directed through 'lures and blocks' by the authorities.

2.2 | Animal movement data

We compiled a total of 519 elephant location points along the elephant trajectory from three different source types. Most of the data (94.6% of the points; Supporting Information: Figure S3) were collected by the Asian Elephant Research Center of National Forestry and Grassland Administration during their drone monitoring of the herd between 23rd September 2020 and 23rd July 2021. Drone

3

monitoring was generally conducted using the model DJI-M300 (Shenzhen DJI Sciences and Technologies Ltd.). The drones were flown at 300–500 m above the elephants and locations were recorded with the drones' "point positioning" function, with an estimated error of generally less than 5 m. This monitoring and data collection was conducted for management rather than research purposes, hence, the number of daily locations recorded was not systematic and it depended on the elephant movements (e.g., if elephants stayed in the same place for many hours, only one point was recorded). This resulted in 1–6 GPS location per day, with some data gap periods (e.g., 4th–15th May 2021; Supporting Information: Figure S3).

We complemented the drone monitoring data with information (2.3% of the points; range: 27th July 2020 to 1st June 2021) from reliable news sources (e.g., photos and videos where we could confidently verify the location). In this case, we used landmarks from the photos or videos and assigned them the geographical coordinates as found in the online mapping service Baidu maps (https://map.baidu.com; Baidu, Inc.). The remaining data (3.1% of the points; range: January 2009 to 5th September 2020) were obtained from "other sources," including photos and videos of the elephants in Mengyang and personal accounts from rangers. Data from "other sources" were geographically less accurate, and we only used them for the broad-scale analysis of movement type, but not for the finer-scale analysis of habitat selection.

2.2.1 | Movement type analysis

To identify the general type of movements of the elephant herd and evaluate whether these movements should be considered as migratory or something else we used a two-step methodology similar to Purdon et al. (2018), analyzing (1) the overlap of seasonal ranges; and (2) net squared displacement (NSD). Our criteria to define the elephant movements as migratory was that both the overlap and the NSD methods classified them as such (Purdon et al., 2018). See Supporting Information: Appendix S2 for details of both analyses.

In the analysis of seasonal range overlap, we considered that the first and second seasonal ranges did not overlap at Bhattacharyya's affinity (BA) index values < 0.15, and high overlap between the first and third seasonal ranges at BA > 0.5 (Purdon et al., 2018). We used the NSD approach to classify the trajectory followed by the elephants within one of the four broad movement types: migratory, dispersal, sedentary, and nomadic (Bunnefeld et al., 2011). This method relies on the straight-line distance between the initial point and subsequent locations of a movement path and allows comparisons between the shape of the actual animal trajectory and the

expected (theoretical) shape for different movement types. We chose the NSD model that best represented the elephant movements by means of model selection with AIC and AIC weights (Burnham & Anderson, 2002).

Climatically, Xishuangbanna has two marked seasons: a rainy season that goes from May to October, and a dry season that goes from November to April. The dry season can be further divided into a dry-cool (November to February) and a dry-hot (March and April) period (Cao et al., 2006). Due to data availability constraints, for the analyses of type of movement, both seasonal range overlap and NSD, we used 1 year of movements starting from 30th May 2020 (the first date for which we had data in the rainy season) to 29th May 2021.

2.3 | Movement characteristics: Habitat use and selection

To analyze the characteristics of the elephant movements and the influence of landscape features on their habitat use and selection, we conducted two types of analyses representing landscape-scale (displacement) and patch-scale (step selection function) spatial scales. For these analyses we only used the high-resolution location data, that is, those from 27th July 2020 to 2nd June 2021, obtained by drone monitoring.

First, we compiled a geospatial data set representing the landscape characteristics of the study area (Table 1 and Supporting Information: Table S1). This data set included variables associated with land use and terrain, the Normalized Difference Vegetation Index (NDVI) and the Tasseled Cap Wetness Index (hereafter "wetness"), nightlight intensity, distance to main roads, and distance to towns and villages. We used covariates from 30 m to 1 km of resolution.

To study broader-scale landscape changes along the elephant path, we analyzed the relationship between landscape covariates and displacement (straight-line distance) from the original home range in Mengyang. Specifically, we used a location known as Wild Elephant Valley, where this elephant herd had frequently been seen since 2009 (Shen et al., 2021) as the starting point for the analysis. We built several models using different combinations of habitat covariates and used the Akaike Information Criterion (AIC) to identify the best model (Burnham & Anderson, 2002). We then used step selection function models (SSF; Thurfjell et al., 2014) to evaluate the elephants patch-scale movement decisions. We selected the best-fitting models using AIC with $\Delta AIC < 2$, we calculated model average for the best candidate models (Burnham & Anderson, 2002), and we estimated the importance of predictor variables by the Sum of Weights (SW; Galipaud et al., 2014).

TABLE 1 List of environmental variables used to evaluate the movements by the elephants in their path to Kunming

Variable name	Resolution	Source
Proportion of forest	30 m	(Jun et al., 2014)
Proportion of cultivated lands	30 m	(Jun et al., 2014)
Proportion of grasslands	30 m	(Jun et al., 2014)
Proportion of shrublands	30 m	(Jun et al., 2014)
Elevation	30 m	Shuttle Radar Topography Mission (SRTM) (GEE)
Global Forest Canopy Height	500 m	(Simard et al., 2011)
Wetness	30 m	Landsat (GEE)
Normalized Difference Vegetation Index	30 m	Landsat (GEE)
Distance to forest edge	30 m	(Jun et al., 2014)
Distance to water sources	Vector data	Open street maps
Mean of nightlight	500 m	Visible Infrared Imaging Radiometer Suite (VIIRS) (GEE)
Global human modification	1 km	(Kennedy et al., 2019)
Distance to cities, towns, and villages	Vector data	Open street maps
Distance to motorway and primary roads	Vector data	Open street maps

Note: GEE refers to products derived using the Google Earth Engine cloud-based platform. For a description of each layer see Supporting Information: Table S1.

2.4 | Body condition assessment

The body condition of wild Asian elephants can oscillate widely, so visual estimates of individuals' body condition scores can be used to assess the health of individuals or the population (Fernando et al., 2009). We used a simple visual system to assess Asian elephant's body condition developed by Wijeyamohan et al. (2015) using both wild and captive Asian elephants. The authors report that they have never found scores above 8 among wild individuals, and that a score of 10 represents obese captive elephants. Two independent and experienced scorers assigned a body condition score to 14 elephants from the Kunming herd using photographs taken in June 2021 (Supporting Information: Appendix S3 and Figure S4). The scores were then averaged for the whole herd. We were unable to obtain images of the elephants from early 2020 for comparative purposes.

3 | RESULTS

3.1 | Type of movement

The Kunming herd moved a straight-line distance (net displacement) of ~300 km from March 2020 to early July 2021, including nearly 200 km between March and June 2021. According to the seasonal range overlap method, the movement of the elephants was classified as nonmigratory, since there was a relatively high degree of overlap (BA = 0.32) between the first and second successive ranges, and a lower degree of overlap (BA = 0.25; Supporting Information: Figure S5) between the first and third seasonal ranges, indicating the herd did not return to the initial seasonal range. The NSD analysis classified the movement of the herd as nomadic behavior (AIC weight = 1; Figure 2a). The migratory model did not converge, and the dispersal and sedentary (home range) models had very low AIC weight (0) compared with the nomadic model. These results indicate that the trajectory followed by the elephants to Kunming cannot be classified as a migratory behavior.

3.2 | Habitat use and preference

At landscape scale, as the elephants moved away from Mengyang, they walked into areas with higher elevation, higher intensity of nightlights, farther away from main roads, and with less forest cover (Supporting Information: Tables S2 and S3).

The SSF analysis showed the complex effects of natural and anthropogenic factors on the elephants' patch-scale movements (Supporting Information: Figure 2b-f; Supporting Information: Tables S4-S6). In their movements, elephants had a complex relationship with forest because, although they avoided areas with greater forest cover (negative effect of forest cover, SW = 1), they preferred areas closer to forest (negative effect of distance to forest, SW = 1). They chose areas of intermediate values of wetness (effect of wetness and wetness²), which indicates preference for areas with intermediate values of habitat structure (in between very thick primary forest and open environments); wetness and wetness², however, had lower support in the models than other variables (SW = 0.58 and 0.41, respectively). Finally, the

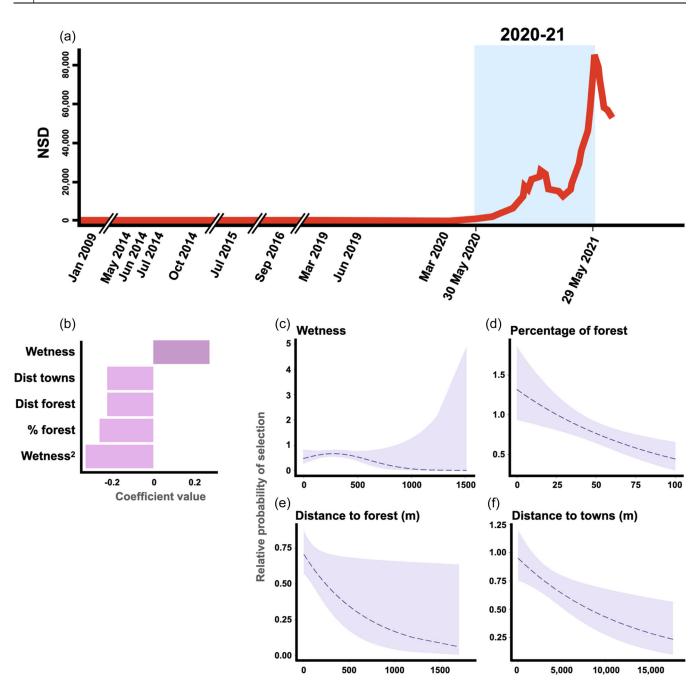


FIGURE 2 (a) Net squared displacement (NSD) of the Kunming herd over time. The reference location (NSD = 0) is "Wild Elephant Valley," in Mengyang. Only the period from 30th May 2020 to 29th May 2021 (blue shade) was used for NSD analysis of type of movement. (b) Normalized coefficients of the environmental variables that affected the fine-scale movements of the elephants as they moved from Mengyang to Kunming; and marginal plots of relative probability of selection in relation to (c) wetness, (d) percentage of forest; (e) distance to forest; (f) distance to towns and villages. Dist, distance.

elephants showed a clear preference for areas with high anthropogenic disturbance (negative effect of distance to towns and villages, SW = 1).

3.3 | Body condition

The overall mean (\pm SD) body condition score (BCS) of the elephants was 7.0 \pm 0 (n = 14 elephants; Figure 3), which represents good health (BCS of 7–8 in this scale represent the best conditions for wild individuals).

4 | DISCUSSION

The movements of a herd of wild elephants from Xishuangbanna to the outskirts of Kunming, several hundred km away, fascinated people all over the world. Elsewhere, we discussed the environmental triggers of this behavior (Campos-Arceiz et al., 2021; see also H. Wang et al., 2021). Here, we analyzed these movements and found that (1) they are consistent with a form of nomadism or dispersal rather than migration; (2) as the elephants moved away from familiar landscapes, they actively chose



FIGURE 3 Side photos of sample elephants from the Kunming herd used to score their body condition. A, adult; BCS, body condition score; INB, infant/newborn; J, juvenile; SA, sub-adult. BCS was evaluated following Wijeyamohan et al. (2015). All photos were taken in June 2021. See Supporting Information: Appendix S3 for details.

to move into areas with high human presence (close to nightlights and towns and villages), rather than into more natural habitats (forest cover), and (3) 15 months after leaving their native home range and venturing into unfamiliar territories, the elephants showed a healthy body condition.

4.1 | Movement type: irruptive nomadism or dispersal, but not migration

The movements of the Kunming herd have often been described as a migration, both by media and experts (e.g., H. Wang et al., 2021). Our results, however, are clear that this behavior should not be considered as migration. Migration is defined by four general features (Glossary; Roshier & Reid, 2003) of which the Kunming herd movements fail to meet three (nonoverlapping ranges, short migratory movements relative to time at seasonal ranges, and temporal predictability). They partially fit the fourth requirement (having symmetrical paths), but this was strongly influenced by the Chinese authorities directing their movements since June 2021. Migratory behavior is expected in highly seasonal environments, but the largely evergreen tropical rainforests of Xishuangbanna are not strongly seasonal.

But, given that the Kunming herd returned to Mengyang, as the XTBG herd had previously done, how should we characterize their behavior? In our NSD analysis, the movements of the Kunming herd were best described as nomadic, and we argue that the behavior of both elephant herds from March 2020 to ~September 2021 can be described as a case of partial irruptive nomadic movements (sensu Teitelbaum & Mueller, 2019; Glossary). Partial because only part of the population (the Kunming and XTBG herds) adopted these movements, while the other herds remained in their home ranges; and irruptive because regular sedentary behavior was punctuated by unpredictable, long-distance movements that were neither seasonal nor dependent on life-stage. Irruptive nomadism can manifest as an escape from abnormally poor conditions, such as the severe drought that hit Southwest China in 2019 and 2020 (H. Wang et al., 2021). Recent progress in animal tracking suggests that irruptive nomadic movements are more common than previously thought (e.g., Dean et al., 2009; Kaczensky et al., 2011).

Until March 2020, the Kunming herd seemed to have a stable home range in Mengyang (we have evidence of their presence there since 2009; Figure 2a). If the herd had established a new home range outside Mengyang, their behavior could have been described as a case of female dispersal, leading to a range shift, like previous events that led to herds from Mengyang establishing in the neighboring areas of Simao, Jiangcheng, and Menghai (black arrows in Figure 1). Dispersal and home range shifts are uncommon for Asian elephant herds, but several cases have also been reported in India (Sivasubramanian & Ramakrishnan, 2021; Sukumar, 2003; Anwaruddin Choudhury pers. comm.) and Indonesia (Gaius Wilson pers. comm.) since the 1990s, usually linked to drastic habitat losses or drought events.

Long-distance female Asian elephant movements, in the hundreds of km, away from their home range are exceptional and we only found evidence of two previous cases, both associated with severe droughts in India (Sukumar, 2003). One took place in 1983, when several herds shifted their home ranges from Tamilnadu and Karnataka into Andhra Pradesh, 200–300 km away, where they had been absent for over two centuries. The other was in 1987, when elephants moved from Bihar to West Bengal, but in this case the elephants did not shift their home range, they just expanded their former one (Sukumar, 2003). In Africa, there are numerous accounts of elephants shifting their home ranges and abandoning protected areas during droughts (e.g., Abraham et al., 2019; Kaszta et al., 2021).

Overall, the movements of the Kunming and XTBG herds are testimony to elephants' ecological and behavioral plasticity, being able to modify their behavior in response to unexpected environmental change. While sedentarism with male natal dispersal is their most common pattern of behavior, elephants' range of potential movement types includes female dispersal, irruptive nomadism, migration (at least in Africa), and nonconforming movement types (e.g., circular movement patterns by elephants in Mali; Wall et al., 2013).

4.2 | Moving close to people and staying in good body condition

As the elephants moved north, the characteristics of the landscapes they used changed considerably from their familiar landscapes in Xishuangbanna. Specifically, the elephants moved into landscapes at higher altitude and higher human presence (nightlight intensity). At finer scale, the step selection function identified somewhat unusual habitat preferences for Asian elephants. In their steps, the Kunming herd actively chose to move close to towns and villages, and avoided areas with high forest cover, while wetness had a moderate influence (Supporting Information: Tables S5 and S6). In Malaysia, where similar step selection function analyses have been conducted (de la Torre et al., 2019, 2021; Wadey et al., 2018), wetness had a stronger influence on their movements, and elephants avoided human presence (negative effect of nightlight intensity). In both environments, elephants avoided moving far away from forests, showing Asian elephants' preference for forest edges (Campos-Arceiz, 2013; de la Torre et al. 2020). We attribute the Kunming herd's preference of moving close to human presence to their loss of fear of people, reliance on crops as food, and the disturbances produced by people along their path, particularly since May 2021.

The high values of the Kunming herd body condition scores are indicative of good health, even a long time after initiating their trip out of Mengyang. The Kunming herd elephants (BCS = 7.0 ± 0 , n = 14) had body condition scores considerably higher and more consistent than elephants in Nangunhe National Nature Reserve (BCS = 5.75 ± 2.4, n=12; Sun et al., 2021), the only other wild elephant population previously assessed in China. The fact that elephants in unfamiliar habitats and moving rapidly over long distances had better body condition than elephants living inside a protected area is testimony to the foraging benefits of feeding on crops as opposed to feeding on wild vegetation in the forest. Additionally, the Kunming herd delivered two babies successfully during their trip. Severe droughts can cause high mortality among elephants (Dudley et al., 2001; Wato et al., 2016). Altering regular movement patterns and moving out of traditional home ranges has been found to mitigate drought-related mortality, at least among calves (Foley et al., 2008). In the case of the Kunming herd, their high body condition scores and successful baby deliveries indicate good health and suggest that the decision of setting off from Mengyang paid off for them.

Our analyses provide a quantitative and solid interpretation of the Kunming herd movements and health condition during their critical time far away from Mengyang and advance our understanding of Asian elephant movement ecology in response to environmental and anthropogenic changes. Our movement data came largely from drone-based monitoring at a resolution of just one to six data points per day. Although not as comprehensive as GPS-collar telemetry, our approach sufficed to address the objectives of this study. To our knowledge, this is also the first quantitative analyses of elephant movements in China. Given the ongoing geographic expansion of the elephant population in China (Bai et al., 2022; Zhang et al., 2015) and the intense fragmentation of human-dominated landscapes in their range (Liu et al., 2017), we encourage the use of GPS-collar telemetry to better understand the spatial dynamics of the population. Studying movements was recently identified as one of the research priorities for elephant conservation in China (S. Chen et al., 2021). For future drone-based wildlife

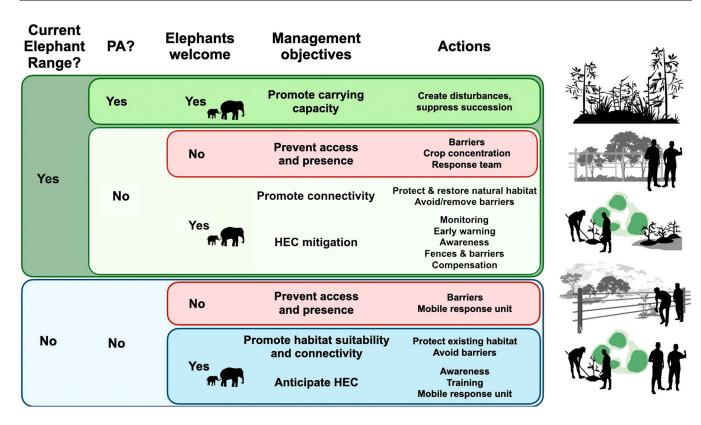


FIGURE 4 Framework of area-based and area-specific measures for Asian elephant conservation in China. HEC, human-elephant conflict; PA, protected area.

monitoring, we encourage the systematic collection of locations at regular periods of time, which is advisable for the analyses of animal movement attributes.

4.3 | Integrating unusual movements into conservation planning

There are important conservation lessons to learn from the movements of the Kunming herd. First, to date, there is no convincing evidence of elephant migration in China (or anywhere else in Southeast Asia). Accordingly, their conservation should be primarily based on area-based and site-specific measures (as corresponds to sedentary animals; Figure 4) such as the new National Park that China is currently planning within elephant range (e.g., S. Chen et al., 2021; Li et al., in press; N. Yang et al., 2021). Since late-succession forest is not an attractive habitat for Asian elephants (e.g., de la Torre et al., 2021; Evans et al., 2018) we recommend introducing small-scale disturbances, such as maintaining a mosaic of early-succession vegetation patches within the forest matrix, which would enhance habitat suitability and elephant carrying capacity within the new park. Such forest gaps provide additional benefits, such as opportunities to monitor the elephant population and to promote conservation-friendly tourism activities. On the other hand, this kind of intervention can lead to a conflict of conservation priorities (i.e., forest vs. elephants) that needs to be carefully considered.

Second, elephants have large home ranges, and they also occupy mixed-use landscapes outside protected areas (de la Torre et al., 2022). Understanding the population distribution and home ranges outside the National Park is important to plan and implement site-specific interventions. As part of the planning process, we recommend identifying "no-go-areas," where elephant presence is considered unacceptable (based on multi-stakeholder decision-making). In areas where elephants are not welcome, elephant access and presence can be prevented using barriers, reducing habitat connectivity, and establishing response units that can drive elephants out of the no-go-areas, if necessary. In areas where elephants are welcome, we recommend two key management objectives (a) promoting connectivity and (b) mitigating human-elephant conflicts (HEC). Connectivity can be promoted by protecting and restoring forest corridors, even in the form of "many small patches", and preventing the development of urban or infrastructure barriers within them. HEC mitigation in China can be approached with a combination of intense elephant monitoring outside protected areas, early-warning systems, safe behavior awareness campaigns, spatial concentration of crops, fences, and financial compensation (see S. Chen et al., 2013; Y. Chen et al., 2016; S. Chen et al., 2021 and Campos-Arceiz et al., 2021 for more details).

Third, since the elephant population in China is expanding, we should expect elephants to continue

dispersing into new, currently unoccupied, areas (Bai et al., 2022). It is important to anticipate these expansions and, again, define "no-go-areas," where elephant recolonization is not acceptable. Where elephants are welcome, we recommend (a) protecting existing suitable habitats and (b) being prepared to mitigate future HEC, for example, by running awareness campaigns, training local officers, and establishing a "mobile elephant response unit" that can be mobilized to assist local authorities in case of elephant arrival. The movements of the Kunming herd, have shown that the scale of elephant movements can be measured in the hundreds of km. Hence, preparedness should be at the same scale.

Fourth, the Kunming herd chose to move close to towns, villages, and nightlight intensity, rather than avoiding them. We interpret this as an indication that the elephants felt safe to move near people and to feed on crops. The strategy of "getting people out of the elephants' way", currently practiced in China (Campos-Arceiz et al., 2021), creates a risk of elephants losing fear of people and becoming reckless, a dangerous situation that may increase the risk of humanelephant encounters and elephant attacks to people. We recommend the use of nonconfrontational methods (e.g., electric fences, permanent barriers) to prevent elephants becoming habituated to crop-based diets and discourage the regular use of so-called "elephant canteens," whereby crops are planted to subsidize elephant diet. Food subsidies should be used only in exceptional circumstances, for example, during drought.

Fifth, the Kunming and the XTBG herds have shown that, in case of severe environmental change, elephants can respond by altering their behavior and movement patterns. This requires temporal preparedness to respond in case of events that might affect conditions in their home range. Examples of such events include droughts, floods, forest fires, and other forms of large-scale disturbance that might affect their habitats and that are likely to increase their frequency with climate change (IPCC, 2021).

Sixth, these lessons, although specific for elephant conservation in China, will become increasingly relevant to other parts of the Asian elephant range, and for the conservation of other large and conflict-prone species. The ongoing expansion of China's small Asian elephant population is associated with climate change, strict protection, and broad-scale socioeconomic changes (Bai et al., 2022). This expansion is taking place in highly developed and fragmented landscapes where close contact and intense conflict with people are inevitable. This scenario, similar to what is happening with large carnivores in parts of China, Europe, and North America (e.g., Chapron et al., 2014; Gompper et al., 2015; T. Wang et al., 2016), will become increasingly common throughout tropical Asia.

5 | CONCLUSIONS

We have analyzed a high-profile case of unusual behavior by a charismatic, endangered, and potentially dangerous animal species. A herd of elephants left their home range in a protected area and embarked in a long journey that took them hundreds of km away from the recent elephant distribution range and into the outskirts of a big city, causing unprecedented economic and management responses. Yet, this journey has paid off for the elephants, which managed to avert the consequences of a severe drought. We identified their behavior as an episode of partial and irruptive nomadic behavior, although it could have been a failed attempt of dispersal (i.e., range shift). We also found that, along their path, the elephants selected habitats with high anthropogenic disturbance (e.g., close to towns and villages and with high nightlight intensity), most likely due to their reliance on crops as food and habituation to contact with people. Landscapes in Southwest China are intensively fragmented and this inevitably affects the elephants' capacity to respond to unpredictable environmental changes, such as drought. Overall, this situation is testimony to elephants' behavioral plasticity and ability to adapt to intensely modified landscapes. We have been able to recommend conservation strategies and actions that fit the type, characteristics, and scale of movements of these elephants, showcasing the importance of integrating movement ecology in conservation planning, particularly for wideranging species. We expect events like this to become more common in China and elsewhere, as conservation policies become more effective and populations recover megafauna in humandominated landscapes.

AUTHOR CONTRIBUTIONS

Ahimsa Campos-Arceiz: Conceptualization; investigation; methodology; visualization; writing - original draft; writing - review and editing. J. Antonio de la Torre: Conceptualization; data curation; formal analysis; methodology; visualization; writing review and editing. Ke Wei: Investigation; writing - review and editing. Xiaoyu O. Wu: Investigation; writing - review and editing. Yang Zhang: Data curation; investigation; writing - review and editing. Yufei Zhu: Investigation; writing - review and editing. Zicheng Yang: Data curation; investigation. Shu Chen: Investigation; writing - review and editing. Yang Bai: Data curation; investigation; writing - review and editing. Richard T. Corlett: Investigation; writing - review and editing. Fei Chen: Conceptualization; data curation; investigation; writing - review and editing.

ACKNOWLEDGMENTS

We thank the Asian Elephant Research Center of the National Forestry and Grassland Administration for the elephant location data; and Yunnan's Forest Fire Department, Xishuangbanna Tropical Botanical Garden, and Mr Cao Dafan for elephant photographs; Tommy Qian, and Heli Ouyang for help in fieldwork; and Lisa Ong for help with the design of the figures.

CONFLICTS OF INTEREST

The first author is Co-Editor-in-Chief of Integrative Conservation. Other authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The elephant movement data is not publicly available but can be accessed upon request to the corresponding authors.

ORCID

Ahimsa Campos-Arceiz http://orcid.org/0000-0002-4657-4216

J. Antonio de la Torre b https://orcid.org/0000-0003-1994-8478

Ke Wei https://orcid.org/0000-0002-7616-3493 *Richard T. Corlett* http://orcid.org/0000-0002-2508-9465

REFERENCES

- Abraham, J.O., Hempson, G.P. & Staver, A.C. (2019) Droughtresponse strategies of savanna herbivores. *Ecology and Evolution*, 9, 7047–7056.
- Allen, A.M. & Singh, N.J. (2016) Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, 3, 155.
- Bai, D., Wan, X., Zhang, L., Campos-Arceiz, A., Wei, F. & Zhang, Z. (2022) The recent Asian elephant range expansion in Yunnan, China, is associated with climate change and enforced protection efforts in human-dominated landscapes. *Frontiers in Ecology and Evolution*, 10, 889077. Available from https://doi.org/10.3389/fevo.2022.889077
- Bunnefeld, N., Börger, L., Van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. et al. (2011) A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology*, 80, 466–476.
- Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. New York: Springer-Verlag.
- Campos-Arceiz, A. (2013) The dangerous myth of the Noble Beast. *Gajah*, 38, 5.
- Campos-Arceiz, A., de la Torre, J.A., Wei, K., Wu, X.O., Zhu, Y., Zhao, M. et al. (2021) The return of the elephants: how two groups of dispersing elephants attracted the attention of billions and what can we learn from their behavior. *Conservation Letters*, 14, e12836.
- Cao, M., Zou, X., Warren, M. & Zhu, H. (2006) Tropical forests of Xishuangbanna, China 1. *Biotropica*, 38(3), 306–309.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H. et al. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517–1519.
- Charif, R.A., Ramey, R.R., Langbauer, W.R., Payne, K.B., Martin, R.B. & Brown, L.M. (2005) Spatial relationships and matrilineal kinship in African savanna elephant (Loxodonta africana) clans. Behavioral Ecology and Sociobiology, 57(4), 327–338.

- Chen, S., Sun, G.Z., Wang, Y., Huang, C., Chen, Y., Liu, P. et al. (2021) A multistakeholder exercise to identify research and conservation priorities for Asian elephants in China. *Global Ecology and Conservation*, 27, e01561.
- Chen, S., Yi, Z.F., Campos-Arceiz, A., Chen, M.Y. & Webb, E.L. (2013) Developing a spatially-explicit, sustainable and riskbased insurance scheme to mitigate human-wildlife conflict. *Biological Conservation*, 168, 31–39.
- Chen, Y., Marino, J., Chen, Y., Tao, Q., Sullivan, C.D., Shi, K. et al. (2016) Predicting hotspots of human-elephant conflict to inform mitigation strategies in Xishuangbanna, Southwest China. *PLoS One*, 11(9), e0162035.
- Choudhury, A. (1999) Status and conservation of the asian elephant *Elephas maximus* in north-eastern India. *Mammal Review*, 29(3), 141–174.
- Davidar, E.R.C., Davidar, P., Davidar, P. & Puyravaud, J.P. (2012) Elephant *Elephas maximus* linnaeus (Proboscidea: Elephantidae) migration paths in the Nilgiri hills, India in the late 1970s. *Journal of Threatened Taxa*, 04(14), 3284–3293.
- Dean, W.R.J., Barnard, P., Anderson, M.D., Dean, W.R.J., Barnard, P. & Anderson, M.D. (2009) When to stay, when to go: trade-offs for Southern African arid-zone birds in times of drought. *South African Journal of Science*, 105(1-2), 24–28.
- Dudley, J.P., Criag, G.C., Gibson, D.S.C., Haynes, G. & Klimowicz, J. (2001) Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology*, 39(2), 187–194.
- Evans, L.J., Asner, G.P. & Goossens, B. (2018) Protected area management priorities crucial for the future of Bornean elephants. *Biological Conservation*, 221, 365–373.
- Fernando, P., Janaka, H.K., Ekanayaka, S.K., Nishantha, H.G. & Pastorini, J. (2009) A simple method for assessing elephant body condition. *Gajah*, 31, 29–31.
- Fernando, P., Wikramanayake, E.D., Janaka, H.K., Jayasinghe, L.K.A., Gunawardena, M., Kotagama, S.W. et al. (2008) Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology*, 73(1), 2–13.
- Foley, C., Pettorelli, N. & Foley, L. (2008) Severe drought and calf survival in elephants. *Biology Letters*, 4(5), 541–544.
- Galipaud, M., Gillingham, M.A.F., David, M. & Dechaume-Moncharmont, F.X. (2014) Ecologists overestimate the importance of predictor variables in model averaging: A plea for cautious interpretations. *Methods in Ecology and Evolution*, 5, 983–991. Available from https://doi.org/10.1111/2041-210X.12251
- Gompper, M.E., Belant, J.L. & Kays, R. (2015) Carnivore coexistence: America's recovery. *Science*, 347(6220), 382–383.
- IPCC. (2021) Climate change 2021: The physical science basis. Contribution of working group i to the sixth assessment report of the intergovernmental panel on climate change. IPCC.
- Jun, C., Ban, Y. & Li, S. (2014) Open access to Earth land-cover map. *Nature*, 514(7523), 434.
- Kaczensky, P., Ganbataar, O., Altansukh, N., Enkhsaikhan, N., Stauffer, C. & Walzer, C. (2011) The danger of having all your eggs in one basket—winter crash of the re-introduced Przewalski's horses in the Mongolian Gobi. *PLoS One*, 6(12), e28057.
- Kaszta, Ż., Cushman, S.A. & Slotow, R. (2021) Temporal nonstationarity of path-selection movement models and connectivity: an example of African elephants in Kruger National Park. *Frontiers in Ecology and Evolution*, 9, 207.
- Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J. (2019) Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology*, 25(3), 811–826.
- Koirala, R.K., Ji, W., Aryal, A., Rothman, J. & Raubenheimer, D. (2016) Dispersal and ranging patterns of the Asian elephant (*Elephas maximus*) in relation to their interactions with humans in Nepal. *Ethology Ecology & Evolution*, 28(2), 221–231.
- Leimgruber, P. & Songer, M.A. (2021) Conservation: where can elephants roam in the anthropocene? *Current Biology*, 31(11), R714–R716.
- Li, L., Wang, Q., Yang, H., Tao, Y., Wang, L., Yang, Z. et al. Mobile animals and immobile protected areas: improving the

coverage of nature reserves for asian elephant conservation in China. *Oryx*.

- Liu, P., Wen, H., Harich, F.K., He, C., Wang, L., Guo, X. et al. (2017) Conflict between conservation and development: cash forest encroachment in Asian elephant distributions. *Scientific Reports*, 7(1), 6404.
- Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A. et al. (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365, 2289–2301. Available from https:// doi.org/10.1098/rstb.2010.0082
- Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments: from individual behaviors to population distributions. *Oikos*, 117, 654–664.
- Purdon, A., Mole, M.A., Chase, M.J. & Van Aarde, R.J. (2018) Partial migration in savanna elephant populations distributed across Southern Africa. *Scientific Reports*, 8(1), 11331.
- Roshier, D. & Reid, J. (2003) On animal distributions in dynamic landscapes. *Ecography*, 26(4), 539–544.
- Seebacher, F. & Post, E. (2015) Climate change impacts on animal migration. *Climate Change Responses*, 2(1), 5.
- Shen, Q.Z., Wang, B., Bao, M.W., Xiao, Y. & Yan, H.L. (2021) A study on monitoring activities of Asian elephants in dry season in the Sanchahe River area of the reserve. *Agriculture and Technology*, 04, 111–114. Available from https://doi.org/10.19754/j.nyyjs.20210228031
- Shepard, D.B., Kuhns, A.R., Dreslik, M.J. & Phillips, C.A. (2008) Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation*, 11(4), 288–296.
- Simard, M., Pinto, N., Fisher, J.B. & Baccini, A. (2011) Mapping forest canopy height globally with spaceborne lidar. *Journal* of Geophysical Research: Biogeosciences, 116(G4).
- de Silva, S., Ranjeewa, A.D. & Kryazhimskiy, S. (2011) The dynamics of social networks among female Asian elephants. *BMC Ecology*, 11(1), 17.
- Sivasubramanian, G. & Ramakrishnan, B. (2021) Habitat assessment and utilization by Asian elephant (*Elephas maximus* L.) in Palani hills Northern slope reserve forests of Dindigul Forest Division, Tamil Nadu, Southern India. *Journal of Science and Technology*, 6(01), 73–82.
- Sukumar, R. (2003) *The living elephants: evolutionary ecology, behaviour, and conservation.* Oxford University Press.
- Sun, Y., Chen, Y., Díaz-Sacco, J.J. & Shi, K. (2021) Assessing population structure and body condition to inform conservation strategies for a small isolated Asian elephant (*Elephas maximus*) population in southwest China. *PLoS One*, 16(3), e0248210.
- Teitelbaum, C.S. & Mueller, T. (2019) Beyond migration: causes and consequences of nomadic animal movements. *Trends* in Ecology & Evolution, 34(6), 569–581.
- Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014) Applications of stepselection functions in ecology and conservation. *Movement Ecology*, 2(1), 4.
- de la Torre, J.A., Cheah, C., Lechner, A.M., Wong, E.P., Tuuga, A., Saaban, S. et al. (2022) Sundaic elephants prefer habitats on the periphery of protected areas. *Journal of Applied Ecology*.
- de la Torre, J.A., Lechner, A.M., Wong, E.P., Magintan, D., Saaban, S. & Campos-Arceiz, A. (2019) Using elephant movements to assess landscape connectivity under Peninsular Malaysia's central forest spine land use policy. *Conservation Science and Practice*, 1(12), e133.
- de la Torre, J.A., Wong, E.P., Lechner, A.M., Zulaikha, N., Zawawi, A., Abdul-Patah, P. et al. (2021) There will be conflict-agricultural

landscapes are prime, rather than marginal, habitats for Asian elephants. *Animal Conservation*, 24, 720–732.

- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C. et al. (2018) Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466–469.
- Vidya, T.N.C. & Sukumar, R. (2005) Social organization of the Asian elephant (*Elephas maximus*) in Southern India inferred from microsatellite DNA. *Journal of Ethology*, 23, 205–210.
- Wadey, J., Beyer, H.L., Saaban, S., Othman, N., Leimgruber, P. & Campos-Arceiz, A. (2018) Why did the elephant cross the road? the complex response of wild elephants to a major road in Peninsular Malaysia. *Biological Conservation*, 218, 91–98.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S. et al. (2021) Human footprint and protected areas shape elephant range across Africa. *Current Biology*, 31(11), 2437–2445.e4.
- Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V. & Douglas-Hamilton, I. (2013) Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation*, 157, 60–68.
- Wang, H., Wang, P., Zhao, X., Zhang, W., Li, J., Xu, C. et al. (2021) What triggered the Asian elephant's northward migration across southwestern Yunnan? *The Innovation*, 2(3), 100142.
- Wang, T., Feng, L., Mou, P., Wu, J., Smith, J.L.D., Xiao, W. et al. (2016) Amur tigers and leopards returning to China: direct evidence and a landscape conservation plan. *Landscape ecology*, 31(3), 491–503.
- Wato, Y.A., Heitkönig, I.M.A., van Wieren, S.E., Wahungu, G., Prins, H.H.T. & van Langevelde, F. (2016) Prolonged drought results in starvation of African elephant (*Loxodonta africana*). *Biological Conservation*, 203, 89–96.
- Wijeyamohan, S., Treiber, K., Schmitt, D. & Santiapillai, C. (2015) A visual system for scoring body condition of Asian elephants (*Elephas maximus*): visual body condition scoring for Asian elephants. *Zoo Biology*, 34(1), 53–59.
- Yang, K.F., Tao, Q., Wang, L.X. & Guo, X.M. (2018) Thoughts on protection and management of wildlife habitat in Xishuangbanna. *Shandong Forestry Science and Technology*, 48(2), 93–96.
- Yang, N., Li, W., Liu, P. & Zhang, L. (2021) China's homeless elephants need linked reserves. *Nature*, 595(7866), 172.
- Zhang, L., Dong, L., Lin, L., Feng, L., Yan, F., Wang, L. et al. (2015) Asian elephants in China: estimating population size and evaluating habitat suitability. *PLoS One*, 10(5), e0124834.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Campos-Arceiz, A., de la Torre, J.A., Wei, K., Wu, X. O., Zhang, Y., Zhu, Y., et al. (2022) China's wandering elephants: Integrating exceptional movements into conservation planning. *Integrative Conservation*, 1–12. https://doi.org/10.1002/inc3.10