

The *Rurban* Elephant: Behavioural Ecology **16** of Asian Elephants in Response to Large-Scale Land Use Change in a Human-Dominated Landscape in Peri-Urban Southern India

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Abstract

An impetus for growth and development in India, with the second largest human population in the world, has resulted in rapid changes in land use across the country, especially over the last two decades. While the land area under agriculture has only slightly increased, there have been significant changes in the shift from single-cropping to double- or multiple cropping every year and an overall increase in built-up areas. We assess the impacts of such transformations on the lives of India's largest land mammal, the Asian elephant, at a time when about 400 people and 150 elephants succumb annually to human–elephant conflict

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across the country. Although elephants generally prefer forested habitats, the increased availability of nutritious crops and forest cover in the form of agroforestry plantations outside protected forests has led them to move extensively across peri-urban areas and successfully adapt to this novel anthropogenic ecological regime. We discuss these unique, inexorable processes of synurbisation, adaptation in a nonhuman species to human-induced change, with a particular focus on how the successful exploitation of *rurban* agricultural resources has allowed for the appearance of spatially and temporally flexible behavioural innovations that, in turn, impact the life-history strategies of a threatened elephant population in a peri-urban region of southern India.

Keywords

Movement ecology · Behavioural flexibility · Synurbisation · Peri-urban agriculture · Human–elephant conflict management

16.1 Changing Landscapes, Shifting Behaviours?

We live in a world that is increasingly urbanising, with the ratio of urban to rural human population decreasing from 1:6.7 in the 1900s to less than 1 today (Bettencourt and West 2010). It is also well documented that the human footprint on the environment, especially its negative impact on global biodiversity is on the rise (Venter et al. 2016). Urban sprawl itself has been predicted to increase from 0.3% of the total land area in 2000 to about 1.1% by 2030, with a concomitant reduction in forested areas (Angel et al. 2007; Santini et al. 2019). Recent studies, however, suggest that the earth is greening (Chen et al. 2019). Although this is a positive development, 82% of the increase in green cover in India has been attributed to agriculture and only 4.4% to forest cover, mostly monoculture plantations (Chen et al. 2019). In addition, linear infrastructure development, of roads and railways in and around forest areas, between 2000 and 2015, has resulted in further fragmentation of wildlife habitats of large ranging mammals, such as the Asian elephant, with more than 90% of the forest patches in India being reduced to less than 1 km² in area (Nayak et al. 2020).

Nonhuman species are known to exhibit behavioural adaptations in response to the environmental constraints they face in their daily lives (Stephens et al. 2007). Studies globally have shown, however, that, in a human-centric world, animals are forced to either adapt to these human-induced changes or perish, a process known as synurbisation (Santini et al. 2019). Animals that can adapt and, at times, even thrive in increasingly urbanised areas are able to vary their time-activity budgets (Sih et al. 2011; Tuomainen and Candolin 2011; Wong and Candolin 2015), search out and feed in nutrition-rich patches such as cropfields and, increasingly in response to anthropogenic pressures, increase their movement rates in human-dominated areas or completely move out of high human-density sites to settle in alternate areas (see Gaynor et al. 2018 for a review). Such novel habitats may also be an ecological trap (Simon and Fortin 2020). This is especially true for large mammals with widespread home ranges that extend across human-dominated areas, such as the Asian elephant,



Fig. 16.1 Forested habitats of elephants are rapidly transforming into agricultural and urbanised areas

which has been known to feed on nutritious crops for more than three decades now (Sukumar 1989; Graham et al. 2009; Srinivasaiah et al. 2019).

The Asian elephant *Elephas maximus* has home ranges varying from 250 to 1000 km², depending on the forest vegetation type and season (Sukumar 2003, 2006; Choudhury et al. 2008). The ranging behaviour of this species in such landscapes across southern Asia is also likely to be influenced by ecological as well as anthropogenic factors (Johnsingh and Williams 1999; Srinivasaiah et al. 2012; Kshettry et al. 2020). Large-scale extraction of resources from natural habitats has resulted in habitat degradation and loss across Asian elephant ranges (Venter et al. 2016), with the consequent depletion of resources for the elephants themselves (Sukumar 1989; Calabrese et al. 2017). Habitat fragmentation has, in fact, been recognised as a major reason for the endangerment of this species, with individual elephants becoming restricted to patchy refuges linked by corridors that are under high conservation threat (Leimgruber et al. 2011; Sukumar 2003). Additionally, human activities such as land use change and poaching have resulted in increased human–elephant conflict, with associated mortalities for both species (Sukumar 2003; Hauenstein et al. 2019).

With human activities expanding into natural forested habitats (Venter et al. 2016), both elephants and humans increasingly find themselves competing over resources (Pimm et al. 1995; Balmford et al. 2001; Sukumar 2003). It is noteworthy that although elephants and humans have possibly shared habitats and resources over centuries now, more recent and extensive changes in land use, mostly the advent of agriculture (Chen et al. 2019), may have significantly impacted the behaviour of elephants (Buij et al. 2007; Graham et al. 2009; Srinivasaiah et al. 2019). In extreme cases, they have even ceased to occur in very high human-density landscapes (Parker and Graham 1989a, b; Eltringham 1990; Barnes et al. 1991; Fay and Agnagna 1991; Happold 1995; Hoare and Du Toit 1999; Buij et al. 2007; Kshettry et al. 2020). An understanding of the impact of such large-scale anthropogenic changes, occasionally even in peri-urban areas (Fig. 16.1), on the behavioural ecology of big mammals, such as elephants, is, however, essential for landscape-level conservation planning, management of forest areas and for human welfare across the Indian subcontinent.

In this chapter, we assess the impact of changing land use and management practices on the distribution of elephants in a human-dominated landscape over a period of 16 years. Our study area spanned the states of Karnataka and Tamil Nadu, specifically the districts of Bangalore, Tumkur, Ramanagara and Krishnagiri. Here,

we first discuss the impact of different resource-availability regimes on the residence time of individual elephants in patches and the influence of biological variables such as gender, age and group type at the population level. We then discuss how the daily activity patterns of male elephants can change, as they transition from a low humandensity habitat, such as a protected forest to a high human-use production landscape. By detailing the modifications in ranging and behavioural decisions made by this population of Asian elephants in a fragmented, largely agricultural landscape of southern India in response to varying levels of resource availability and human activity, we intend to showcase the behavioural adaptability of elephants that can help them persist in the *rurban*.

16.2 The Study Landscape and Its Elephants

Our study landscape, spanning over 10,000 km², comprised several Protected Areas (PAs) including the Bannerghatta National Park and Cauvery North Wildlife Sanctuary, and their surrounding human-dominated areas in the districts of Bangalore, Ramanagaram, Tumkur and Krishnagiri in the states of Karnataka and Tamil Nadu with an average density of ~350 people/km² (Census 2011; Srinivasaiah et al. 2012, 2019). The terrain in this landscape is highly undulating, with a mean altitude of 865 m above mean sea level and an average annual rainfall of 937 mm. The vegetation within the forest ranges from predominantly deciduous to scrub woodland with riparian patches along the streams (Srinivasaiah et al. 2012). Geographically, the PAs are contiguous with larger patches of forests located southeast and southwest, forming part of the Nilgiris—Eastern Ghats Elephant Reserve. More importantly, what concerns us here is that the PAs are surrounded by well-irrigated croplands and human settlements that dot the landscape (Anand et al. 2009).

The high-density human population in and around these PAs largely comprise subsistence farmers, livestock-grazers, and manual labourers engaged in sand-mining and granite-quarrying. The communities depend on the forests for their non-timber forest produce, firewood and livestock-grazing. Amongst the farming communities, the majority are marginal farmers practicing subsistence agriculture alongside farmers who grow commercial crops and have plantations. The Pas have distinct dry and wet seasons with a mean monthly rainfall of 5 mm in January and 170 mm in October, receiving both the southwest and northeast monsoon rains in most years (Srinivasaiah et al. 2019, in press).

The study landscape was classified into different land use types, based on geospatial data obtained from the National Remote Sensing Agency of the Government of India (downloaded from http://bhuvan3.nrsc.gov.in/cgi-bin/LULC250K. exe). The original 19 Land Use and Land Cover (LULC) categories (NRSA 2006) were merged to derive eight LULC categories: Deciduous Forest, Degraded Forest, Plantation (including orchards), Crop (seasonal and multicrop), Current Fallow, Wasteland, Waterbody, and Built-Up Area (Fig. 16.2; Srinivasaiah et al. 2019). Within a smaller area of ~350 km², known to be an area of intense use by elephants within the larger landscape, a detailed assessment of resource availability and threats



Fig. 16.2 Map of the study landscape in southern India showing LULC types at 55-m resolution and the important urban centres of the region

was undertaken. The maximum average values of Normalised Difference Vegetation Index (NDVI) and Leaf Area Index (LAI) were extracted with MODIS data products, using Quantum GIS (QGIS 2009) and Geographic Resources Analysis Support System (GRASS 2007) and their values, obtained during the observation period, used as surrogate measures of forage (Druce et al. 2008; Okello and D'Amour 2008; Young et al. 2009) and shade availability, respectively. The values of NDVI, LAI, Number of Waterbodies per 4 km² Area and a Human Disturbance Index (encounter rate of human- or human-associated disturbances × proportion of sampling segments in which these disturbances were found) were thus, respectively, used as surrogate measures of the four study variables: forage, shade, water and human presence. Quantile classification was used to classify each of the four variables into low, medium and high strata, with their cut-off values being distributed such that the entire study area was classified into equal numbers of low, medium and high strata for each variable.

The Asian elephant has been estimated to number 35,000–50,000 individuals, spread across a range of 13 Asian countries (Blake and Hedges 2004). India has approximately 50% of the total population of the species (20,000–25,000), with southern India supporting around 10,000 elephants in the wild (Project Elephant 2017). Traditionally, significant levels of hunting and poaching for tusks, and, increasingly, habitat loss, fragmentation and degradation of habitats have led to a drastic decline in elephant populations, with the species currently endangered

(Choudhury et al. 2008). The estimated density of elephants in our study landscape was 1.0 elephant km^2 (Project Elephant 2017).

The study population consisted of 78 individuals, distributed in 13 herds, 4 all-male groups and 12 solitary males, roving over an area of $\sim 600 \text{ km}^2$. The population-level analyses that we conducted were based on demographic data collected from all the individuals across all the dry and wet seasons since 2009. In addition, 25 adult (>20 years of age) and subadult (10–20 years of age) males, representing a subset of these 78 individuals, were observed more closely, between 2009 and 2015, in an area of $\sim 80 \text{ km}^2$, comprising a PA and a human-use agricultural area (HA). The land use characteristics of the HA and PA have been depicted in Table 16.1.

The observed elephants were classified into three group types, namely solitary or single male elephants; all-male group (AMG), a coalition of male elephants alone; and herd, consisting of one or more family units. Individual elephants were grouped into four age classes: adult (>15 years), subadult (5–15 years), juvenile (1–5 years) and calf (<1 year). Data on diurnal activity of elephants was collected using instantaneous scan sampling, in which all visible individual male elephants, in herds, all-male groups or as solitary, were scanned once every 15 min in order to record six mutually exclusive behavioural states, namely Feeding, Moving, Standing, Watering, Socialising and Other Behaviours (Altmann 1974). Behavioural observations of elephants at night in the HA, however, were conducted using extensive ad libitum sampling. Moreover, we conducted a total of 3628 instantaneous scans of demographic structure and behavioural states of all individuals in our study population, once every 15 min during the observation periods, to assess the intensity of habitat use, total range area and distribution patterns. We used the G-test of independence to compare the behavioural activities of elephants across different age-gender categories, habitat variable strata and seasons of the year, while the Wilcoxon rank sum test was employed to compare behavioural profiles between different habitats in the study landscape.

16.3 Life in an Urbanising Landscape

Elephant populations mostly occur in high densities within well-established PAs across the Indian subcontinent (Jathanna et al. 2015); these constituted about 51.8% and a meagre 1.9% of the PA and HA in our study landscape, respectively. The rural areas, with cropfields, forest plantations and grazing pastures, covered over 60% of the land area. Often adjacent to populous human habitations, these are known to provide adequate space and resources to accommodate a wide array of wildlife that live alongside burgeoning human populations (Western et al. 2009). It is important to note that cropfields accounted for approximately 18.33% of our study area, a significant proportion of this being peri-urban in nature, adjacent to several important urban centres such as Bangalore and Hosur of southern Karnataka and western Tamil Nadu, respectively. Moreover, degraded forests, scrublands, rocky areas and culturable wastelands, among others, amount to more than 15% of the total

Table 16.1 LULC character	istics of the H	Human-use	Agricultural Ar	ea (HA) and	the Protected F	orest Areas (P/	As) in the stuc	iy landscape		
	Mean perce	entage	Minimum pe	rcentage	Maximum p	ercentage	Standard de	viation	Standard	error
Cell LULC characteristic	HA	PA	HA	PA	HA	PA	HA	PA	HA	PA
Built-up area	3.01	7.12	0.97	0.00	5.02	22.74	2.05	10.52	1.03	5.26
Crop	21.15	15.50	17.12	3.59	25.25	33.69	04.55	13.05	2.27	6.52
Current fallow	0.83	1.48	0.22	0.07	1.32	4.67	0.56	2.16	0.28	1.08
Deciduous forest	1.90	51.80	1.34	34.88	3.00	67.52	0.75	18.02	0.38	9.01
Degraded forest	0.10	7.50	0.02	2.95	0.22	12.28	0.10	4.39	0.05	2.20
Plantation	56.60	3.27	47.96	1.39	62.55	6.06	6.39	2.11	3.19	1.05
Wasteland	0.27	13.00	0.00	9.51	0.61	14.89	0.31	2.37	0.16	1.18
Waterbody	16.15	0.37	9.90	0.00	22.47	0.75	5.13	0.43	2.57	0.21

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Fig. 16.3 Herds and adult male elephants preferably reside in forested habitats but are increasingly moving to inhabit other land use types, such as cropfields, grazing pastures and peri-urban or even urban areas

geographical area of the country (State of Indian Agriculture 2016). These, often human-dominated, areas harbour elephants as well, even though elephant populations may be in significantly lower densities (Srinivasaiah et al. 2019). Thus, elephants can choose from a diverse ecological and anthropogenic setting to spend their time in (Fig. 16.3).

16.4 Decision-Making in a Dynamic Natural-Anthropogenic Landscape Matrix

As rainfall is seasonal in our study area, occurring only from late May to early October, a change in forage quantity and quality is expected across the year. Such a change in forage quality was indeed reflected in the increase in NDVI across the dry and wet seasons during our study (*G*-test of independence, G = 44.215, df = 2, p = 0.000). Conversely, although the local streams flow mostly during the wet season within the park, there was no change in water availability detected across the two seasons. This could be attributed to the numerous waterholes constructed by the state Forest Department. Human activity in the farmlands neighbouring the forests usually increases during the monsoon or the wet season subsequent to the cultivation of subsistence crops. Plantation farming, however, was prevalent throughout the year and there was no substantial variability in human presence or preoccupations observed in the study area across seasons (Surface water: G = 0.368, df = 2, p = 0.804; Human activity: G = 0, df = 2, p = 0.054).

Asian elephants, given their slow metabolic rates and large body size, usually need to forage over long periods of time, often up to 18 h a day, feeding on up to 200 kg of food daily (McKay 1973; Sukumar 2003; Srinivasaiah 2019). Our analysis revealed that the ranging behaviour of the study elephants was indeed primarily driven by the availability of forage-rich sites in the landscape, followed by the occurrence of human activities and availability of water. The tracking of forage-rich sites was more prominent during the dry season than in the wet season, with water being the least influential parameter governing elephant movement patterns or habitat use in the landscape across the year. The degree of shade availability was strongly positively correlated to forage availability and hence, not analysed further.

Elephants spent their time (100%) exclusively in the high-forage areas during the wet season, but only 64% of their time in the dry season, a significant difference (G = 1883.091, df = 2, p = 0.000). In response to human activity levels, elephants used the low-human-activity areas significantly more during the wet than in the dry season (G = 267.398, df = 2, p = 0.000). Their usage of the high-human-activity areas, however, remained the same across seasons. In response to the distribution of water, as could be expected, the study elephants used high-water-availability areas significantly more during the dry season than in the monsoon (G = 1217.448, df = 2, p = 0.000).

In support of our initial findings, we observed the study elephants to preferentially seek out high-forage areas during the dry season, in which they spent 64% of total observed time; forage was thus of prime importance to the elephants in the region. In the wet season, however, they spent significantly more time in low-human-activity areas, which accounted for 35% of the study area. This indicated that if forage was available in areas without human presence, such areas would be chosen by the elephants over human-use areas; overlap in resource use with humans was thus avoided. These results provide evidence of a trade-off between resource acquisition and risk avoidance displayed by the elephants in this region.

16.5 Decision-Making in Novel Human-Dominated Habitats

The elephants in the study landscape typically exhibited important behavioural adaptations at the level of the population, manifest principally in age-, gender- or group size-based differences in seasonal habitat use, but also at the individual level through the display of idiosyncratic behaviours (Srinivasaiah et al. 2012).

A comparison of the decisions made by the two genders, for example, revealed that female elephants, represented in our study by herds or mixed-sex groups, adopted a more risk-averse strategy (Sukumar and Gadgil 1988), with their occurrence and duration of stay limited to habitats with the best available natural resources but least human activity. The males, in contrast, (G = 490.874, df = 2, p = 0.000), foraged across a spectrum of land use and anthropogenic activities, their decisions possibly dependent on the particular stage of their life history (Sukumar and Gadgil 1988; Chiyo et al. 2011; Srinivasaiah et al. 2012). Sexually and socially immature males, for example, were probably influenced by their mothers to range in



Fig. 16.4 Female elephants usually adopt a risk-averse strategy by ranging in areas with requisite forage availability but least human activity

low-human-activity areas, such as the forests, while the sexually mature but socially immature adolescent males and the sexually and socially mature adult males moved between the resource-rich cropfields and the forests, the latter especially when in *musth* to mate with the females.

The general strategy of female elephants is to be risk-averse while seeking out requisite levels of forage availability (Fig. 16.4). This phenomenon changes in the dry season when forage levels are typically low. The study herds then tended to occur in medium-forage-medium-human-disturbance areas (G = 357.459, df = 2, p = 0.000). Most high-forage areas during the dry season were cropfields and plantations with high-human activity, as compared to the medium zones with least variability, both in resource availability and threats. Females typically used medium-forage-medium risk areas as a strategy to ensure access to now-scarce resources although they faced the unavoidable risk of encountering humans—a threat to themselves as well as their dependent calves and juveniles (see also Baskaran 1998). This decision was in stark contrast to that shown by the males, who invariably sought out high-forage areas across seasons, regardless of the threat levels involved (Fig. 16.5, G = 0.92, df = 2, p = 0.608).

16.6 Elephants of the Rurban

Although the study elephants, particularly females in herds, generally avoided high human-use areas in the landscape for most of the year, they often ranged across cropfields and fragmented forest habitats during the cropping season. More than half of the annual location data points of females were thus confined to these areas for 3 months in a year, between November and January. This is also the time when crops such as *ragi* or finger millet are in their vegetative stage, ready for harvesting. Males,



Fig. 16.5 Male elephants often adopt a high-risk strategy by ranging in areas, typically cropfields and human habitations, with high-forage availability, irrespective of human activity levels

Period	Years	MCP estimate (km ²)	KDE estimate (km ²)
1	2000-2001	1034.23	3126.25
2	2002–2003	506.53	3006.56
3	2004–2005	1919.61	5279.70
4	2006-2007	1706.73	2212.81
5	2008–2009	1093.36	1403.41
6	2010-2011	3620.96	693.48
7	2012-2013	1650.66	2742.54
8	2015-2016	3649.70	5543.49

Table 16.2 Minimum convex polygon (MCP) and kernel density estimates (KDE) of the home range size of the study elephant herds between 2000 and 2016

however, typically ranged outside forested areas and across cropfields throughout the year (Srinivasaiah et al. 2019).

Asian elephants are known to vary their range depending on the habitat characteristics and resource availability. They have also been observed to disperse from their natal ranges to move to a different region in response to climatic events such as El Niño, characterised by reduced rainfall and drought-like conditions, or La Niña, with its cyclones and increased rainfall, especially in the Indian context (Sukumar 2003). We estimated the range area of our study elephant herds by tracing the movement patterns of 47 adult females, resident in these herds and constituting about 60% of the 78 individual elephants being monitored, during the period from 2000 to 2016. They ranged over a mean (\pm SE) area of 1897.72 (\pm 411.12) km², as obtained through the minimum convex polygon (MCP) method or 3001.03 (\pm 601.15) km², as per the kernel density estimation (KDE) technique, during these years (Table 16.2, Fig. 16.6); the maximum range size recorded was in 2015–2016.



Fig. 16.6 Kernel density estimates (KDE) of the home range size of the study elephant herds over a time period of 16 years, between 2000 and 2016, with each Period consisting of 2 consecutive years (Periods 1–8, Table 16.2)

The variation in the intensity of use of the landscape across land use types by the study elephant herds, both inside the protected forest areas and in the humandominated landscape surrounding the forests, from 2000 to 2016, is shown in Fig. 16.7. There was a significant eastward expansion in herd movement primarily outside the forested areas, with an increase in ranging in the highly fragmented forest patches, during three periods—2004–2005, 2010–2011 and 2015–2016—that appeared to mark critical points in the ranging decisions of female elephants in this population (Sukumar 2003).

The female-led herds typically spent October to February in the western regions of the study landscape, in and around the Bannerghatta National Park, until 2003–2004, after which they began to move eastwards and explored the areas adjoining the Cauvery North Wildlife Sanctuary. By the end of 2016, a complete switch in the annual temporal usage of the landscape had set in, with the study population spending October to March in the eastern regions of the study landscape, having increased their range almost three times since 2003–2004. One of the most important factors promoting this movement in the short term appeared to be the "drives"—the long-distance driving away of elephants from the Bannerghatta National Park to the forests down south, in order to reduce human–elephant conflict in the western parts of Bannerghatta, close to the city of Bangalore, the IT capital of India (Manjunath NB, pers. obs.).



Fig. 16.7 Heat map showing the distribution and intensity of use of the landscape by the study elephant herds during Periods 1–8, from 2000 to 2016

While these drives may have helped elephants explore new habitats, a significant factor that influenced this decision to establish themselves in the eastern parts of the region in the long term appeared to be the land use changes in their distribution range. Monoculture plantations increased from 2.8% in the period 1973–1992 to 5.3% in 1992–2007 across the landscape (Adhikari et al. 2015), with a concomitant reduction in the crop-growing areas in the western parts of our study area, bordering the Bannerghatta National Park. An inexorable process of rurbanisation, defined as the gradual appearance of the economic characteristics and lifestyles of an urban area in a landscape that retains its essential rural features, had begun (Sorokin and Zimmerman 1929; Parsons 1949). A boom in real estate value in the region, due to its proximity to the rapidly urbanising city of Bangalore, resulted not only in a number of farmers selling their land but also an increase in out-migration of famers to work as landless labourers in the neighbouring towns. These lands were either converted to industrial or residential layouts or were planted with fast-growing commercial agroforestry crops, such as Acacia or Eucalyptus, as they did not require much maintenance. It has been suggested that such a change from subsistence crops to plantation cropping may have partly been due to frequent crop damage by elephants from the Bannerghatta National Park (Adhikari et al. 2015). It is also true, however, that there was a long-term reduction in forest area from 53% to about 26% and a concomitant increase in scrub forest area from 0.55% to 15% in the eastern regions of the study landscape between 1920 and 2015 (Ramachandran et al. 2017). Although the extent of agriculture had remained more or less constant at 45-46% during this period, a significant change from single rain-fed cropping to multiple groundwater-aided cropping, augmented by canal-based irrigation, had possibly made this region a more attractive habitat for elephants. Simultaneously, however, their natural habitats were being lost, with nearly 0.08% of the forest area having been diverted to agriculture in this region by 2005 (Ramachandran et al. 2017).

The western regions of the study landscape have become increasingly unsuitable for our study population in the recent years. This is mostly due to change in land use in these areas—from agriculture to plantation crops that are not fed upon by elephants, persistent increase in built-up areas and human densities, construction of animal-proof fences and trenches along the protected areas to prevent elephants from entering cropfields, and the regular adoption of more active measures such as elephant drives. The study elephants have thus found better foraging grounds in the eastern parts of the landscape. With an increase in agriculture to meet their foraging needs and the availability of scrub forest to take refuge in, these elephants seem to have also found safety in and around the forests of the Hosur Forest Division since 2008. The relatively higher values of the KDE over the MCP estimates in our analyses constitute a clear indication of scouting behaviour by the study elephants, a behavioural strategy adopted to perhaps explore and acquire better knowledge of the eastern regions of the landscape.

16.7 The Rurban Male Elephant

In polygynous species, the physical and physiological condition of males often determine their positions in the dominance hierarchy and influence the outcome of intrasexual competition (Poole 1987; Rasmussen et al. 2007; Chiyo et al. 2011).

Male elephants need to build body mass, come into the energetically demanding state of *musth*, and seize opportunities to mate—reproductive demands that require them to continuously track both forage and females (Poole 1982).

Solitary males in *musth* in our study population tended to occur along with oestrous females in their herds. The relatively younger males were also primarily observed within PAs and other forests as they associated with the herds. It is noteworthy that a number of adolescent and older males, nevertheless, continued to frequent agricultural, human-use habitats outside the forested areas. Male Asian and African elephants are known to inhabit agricultural cropfields primarily to forage on the available crops (Sukumar 1989; Chiyo et al. 2012). As dominance in male elephant society is usually determined by *musth* and body condition (Chelliah and Sukumar 2013), individuals could use a high-risk high-gain strategy by feeding on nutritious crops to improve their body condition (Pokharel et al. 2017). In support of these earlier suppositions, we indeed observed a number of males in the human-use areas to be in excellent body condition.

Our studies on rurban male elephants have led to the important discovery of a significant number of all-male groups, primarily distributed at relatively high frequencies in the intensely human-dominated agricultural regions of the study landscape, particularly around the peri-urban areas of Tumkur, Ramanagaram and Hosur (Srinivasaiah et al. 2019). The remarkable adaptability of these all-male groups of elephants is best exemplified by a group of 11 male elephants that ranged in a large expanse (~10,000 km²) across a rurban landscape, about 100 km to the west of the Bannerghatta National Park (Srinivasaiah et al. 2016).

A comparative analysis of the diurnal time-activity budgets of the 11 male elephants in the HA and that of 18 adult males that ranged exclusively in the PA indicated that the former spent a mean (\pm SE) of 2.54 (\pm 0.28)% and 6.95 (\pm 0.69)% of their time Feeding and Moving in contrast to 40.93 (\pm 3.08)% and 39.55 (\pm 3.10)% displayed by the latter, respectively. These differences are statistically significant (Wilcoxon rank sum test, W = 0, n = 29, p = 0.000 for both behaviours). The males in the HA, however, spent a relatively high proportion of their time budget in Standing (42.42 \pm 0.55%), Watering (24.87 \pm 0.68%) and Socialising (18.56 \pm 0.52%). These behavioural states (together with Other Behaviours) were cumulatively exhibited by the males of the PA only to a meagre extent of 19.52% of their total time, these proportions also being significantly different (Standing and Watering: W = 198, n = 29, p = 0.000; Socialising: W = 187, n = 29, p = 0.000; Other Behaviours: W = 196, n = 29, p = 0.031).

It is, however, striking that the proportion of observed time spent Feeding $(53.83 \pm 1.07\%)$ and Moving $(40.43 \pm 1.13\%)$ by the 11 males in the HA increased significantly during the night. The diurnal time-activity budget of individual male elephants in the HA departed significantly from that exhibited by individuals in the adjacent PA. In the HA, the elephants were highly spatially restricted by human threats, at least during the daytime. These males thus often took refuge in village waterbodies and agroforestry plantations during the daylight hours (Srinivasaiah 2019). Feeding and moving then became largely nocturnal, when human activities reduced, and the elephants could feed on the unguarded crops. The proximity of



Fig. 16.8 Changing behavioural strategies of the study elephants across the day in humandominated habitats

these males to one another in spatiotemporally restricted areas, such as waterbodies, surrounded by human habitations, may have also facilitated increased social interactions between these individuals, not typically seen in the males within the PA (Fig. 16.8).

In the resource-rich HA, we speculate that the spatiotemporal restrictions due to human presence and the perceived risks from them may have also compelled the study male elephants to coordinate their behavioural activities and move together as a single unit while they foraged on high-risk cultivated crops. This is supported by our observation that male associations displayed significantly low inter-individual variance in the proportion of time spent in the important behavioural states in the HA (Srinivasaiah, unpubl. obs.). In contrast, males in the PA, with little or no human presence, were free of such risks, and hence showed higher variance in their timeactivity budgets. The importance of perceived risk from humans in determining the behavioural activities of the study elephants was also supported by our observation that at night, when human presence was minimal in the HA, the study elephants exhibited relatively greater variability in the proportion of time spent in different behavioural activities, notably feeding and moving (Srinivasaiah, unpubl. obs.).

16.8 Conclusions: The Synurbised Asian Elephant

Elephants are known to range across large areas in search of resources, such as food and water (Baskaran and Desai 1996). These behavioural activities were under threat in the human-dominated habitats often occupied by our study elephant population. Living in these high-risk areas, however, had their own benefits, mainly in the form of nutritious, human-origin food resources. In order to successfully persist in these areas, therefore, male Asian elephants needed to be strategic and adapt to the prevailing anthropogenic ecological regimes through processes of synurbisation. Solitarily pursued trial-and-error methods of habitat exploration could prove to be costly, as the landscape, such as the one inhabited by our study elephants, was



Fig. 16.9 A young adult male elephant, which died from a fractured leg after falling into a storm water drain in the Bangalore Urban district of Karnataka state

crowded with linear intrusions, including highways, rail lines, innumerable electric wires and trenches that could prove fatal to individual elephants on the move (Fig. 16.9; Nayak et al. 2020).

The increasing agroforestry practices in the villages across the study landscape facilitated the elephants to approach human habitations, as they often used these patches as resting sites during their movements (Krishnan et al. 2019; Srinivasaiah 2019). Moreover, the availability of highly nutritious crops throughout the year led to the rapid escalation of the frequency of visits and duration of stay by elephants in human-dominated areas, with concomitant damage to different crops often ranging from 20% to 50% (Agrawal et al. 2016). In several instances, young adult and adolescent male elephants, who we refer to as the millennial males (Srinivasaiah 2019), have even become resident in these areas. The crop-loss claims, consequent to elephant depredation and registered under the state Forest Department on the eastern side of Bannerghatta, has increased from 2 to 1500 between 2000 and 2010, a staggering 750-fold increase in a decade. Such a drastic increase in the levels of mostly antagonistic interactions between people and elephants is unfortunate, as the conflict is consumptive in nature and seriously impacts rural livelihoods, threatening the food security of the closely adjoining urban areas in the process (Agrawal et al. 2016). Moreover, encounters between the two species often become critical, with approximately 400 people and 150 elephants succumbing to human–elephant conflict across the country annually.

The novel, but stable, all-male groups of elephants, with relatively large numbers of young adult and adolescent individuals, which have begun to emerge recently, appear to constitute a new form of social organisation in the species, possibly in response to highly fragmented habitats with poor inter-patch connectivity (Srinivasaiah et al. 2019). Individuals in these all-male associations seem to coordinate their behavioural activities and strategies in such a way that it promotes more efficient crop-foraging behaviour in the high-risk, high-resource areas. While associating in all-male groups, we believe, could be an adaptive, synurbic social strategy (Srinivasaiah et al. 2019), elephants in regions of intense human use, including rurban or peri-urban areas, may, in addition, even need to modify their proximate behaviours, such as change their circadian rhythms, thus becoming more behaviourally active at night. Finally, it is entirely possible that such behavioural coordination could, in the future, lead to the establishment of stable cultural traditions in elephants that typically inhabit these rapidly evolving anthropogenic landscapes.

We have clearly seen that our study elephants prefer forage-rich sites, while displaying significant flexibility in the selection of these sites across the study landscape, be they natural forests or cropfields. Such remarkable behavioural flexibility, manifest also in the dramatic modification of short-term behavioural patterns or long-term life-history strategies, and developed within the lifetime of individuals, makes elephants one of the most resilient mammalian species on earth. Indeed, it is this very adaptable nature of elephants that may help them survive climate change and other perils of the Anthropocene (Kanagaraj et al. 2019). This is also reminiscent of strategies, such as finding new refugia, which ancestors of the modern-day elephant may have explored in order to survive mega-extinction events of the past (Davis et al. 2013). The movement of elephants to explore novel ecological regimes, due to destruction or fragmentation of their current home ranges, as observed in our study population, is not devoid of human–elephant conflict, especially as more forest habitats are lost or diverted to non-forest land use.

It is imperative that a holistic elephant management plan takes into account the negative human influences on natural environments that challenge or otherwise threaten the lives of individual elephants. The conservation of most elephant populations across the Indian subcontinent, endangered as they are by the obtrusive presence of humans and their various anthropogenic activities, must also incorporate, more ideally, non-human-centric land use planning and landscape design if at all we desire to survive into the future alongside this remarkable species with which we have shared the planet since times immemorial.

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