Ranging and Spacing Behaviour of Asian Elephant (*Elephas maximus* Linnaeus) in the Tropical Forests of Southern India

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Abstract

Larger body mass and associated life history traits of large mammals pose high risks of anthropogenic extinction. Given the wide ranging nature and the synergistic impacts of habitat loss and fragmentation, the living elephants are among the most threatened mammals in the world. Therefore, information on ranging and space use pattern are extremely important for conservation planning, especially in the case of long-ranging species. We studied the ranging and spacing behaviours of Asian elephant (*Elephas maximus*) radio-collaring three clans and two bulls between 1991 and 1995 in Nilgiri Biosphere Reserve, southern India, to understand their implications for conservation. Home-range size varied considerably among the clans (range 562–800 km²), bulls (range 211–375 km²), and between them. Clans ranged over larger areas (mean 677 \pm 69 km²) compared to bulls (293 \pm 82 km²). Clan ranged in degraded, poor quality habitat with low annual rainfall had larger home range (800 km²) than those ranged in high rainfall optimal habitats (562 km²). The smaller home ranges of bulls were possibly due to nonrepresentation of *musth* during the study period. The dry season

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movements of the clans and the bulls were restricted around the perennial water sources, while the wet season movements were extended to areas with temporary water sources. Seasonal home ranges of clans were large during wet seasons $(401 \pm 64 \text{ km}^2)$ than in the dry season $(308 \pm 20 \text{ km}^2)$. On the other hand, bulls ranged over larger areas during the dry season $(231 \pm 47 \text{ km}^2)$ than in the wet seasons (141 \pm 35 km²). All the clans (excepting one) and bulls showed strong fidelity to their home and seasonal ranges. One of the clans shifted its range during the second year of the study. This clan had a major part of the range in the reserved and revenue forests areas, which continued to experience severe biotic pressure resulting in devoid of access to perennial water source. Therefore, the home-range shift of this clan could be attributed to habitat loss and degradation of major parts of its original range. Clans, unlike bulls, appeared to space themselves out and mostly avoided meeting each other, despite extensive overlap in space. Observations on interclan interactions further suggest that there is hierarchy among clans in space use. Such a hierarchy and its resultant spacing among the overlapping clans influence the seasonal habitat use pattern, which in turn could result in dominant clans having priority access to good quality habitat and food, thereby show better survival and reproductive success.

Keywords

Asian elephant · Fidelity · Home range · Hierarchy · Spacing

15.1 Introduction

Larger body mass and associated life history traits of large mammals pose high risks of anthropogenic extinction. Given the wide ranging nature and the synergistic impacts of habitat loss and fragmentation, the living elephants are among the most threatened mammals in the world. Therefore, information on ranging and space use pattern are extremely important for conservation planning, especially in the case of long-ranging species. Movements of an individual or a group of animals are generally restricted to an area named as home range or territory. Seton (1909) had originally suggested the concept of home range. Burt (1943) defined it as that area traversed by the individual in its normal activities of food gathering, mating and caring for young. This excludes the area of uncharacteristic and erratic wanderings outside the normal range. Earlier studies on the home range of elephants in Africa (Douglas-Hamilton 1972; Leuthold 1977; Viljoen 1989a) and in Asia (Easa 1988; Sukumar 1989; Desai 1991) were based on re-sighting individually identified elephants based on the natural characteristic features. This method has severe limitations when studying elephants, which range over large areas and dense wooded forests, especially in Asia. Difficulties in re-sighting the same individual on a regular basis result in inadequate sample size to define home range reliably. To overcome this problem, VHF telemetry came as a handy tool, which has been widely used to study the ranging behaviour of elephants in Africa (Douglas-Hamilton 1972; Leuthold and Sale 1973; Leuthold 1977; Dunham 1986; Viljoen 1989a, b; Thouless

and Dyer 1992; Thouless 1995, 1996; Tchamba et al. 1995; De Villiers and Kok 1997). In Asia, Olivier (1978) first used telemetry; thereafter, only in the recent past there have been studies that are more detailed on the ranging behaviour of elephants using telemetry (Baskaran et al. 1995; Joshua and Johnsingh 1995; Desai and Baskaran 1996; Baskaran 1998).

One of the major drawbacks of the studies on ranging behaviour has been the inability to ascertain how a home range can be reliably defined. Some studies on home range of elephants in Africa (Leuthold 1977; Viljoen 1989a; Thouless 1996; De Villiers and Kok 1997) and in Asia (Baskaran et al. 1995) used location-area curve to examine whether the home range has been well defined. With increasing sample size, an increase in range reaches an asymptotic value. Most studies on Asian elephants (Sukumar 1989; Easa 1988; Desai 1991) have not used this method, and this coupled with low sample sizes has often resulted in an underestimation of home range. There is thus a lack of detailed information on ranging behaviour for many of the Asian elephant population. Information on ranging behaviour is essential primarily to provide adequate space for long-term conservation of the species and in designing the protected areas so that administrative boundaries can coincide with ecological boundaries. This information is especially crucial for species like elephant that range so widely and in conflict with humans frequently due to continual loss of their ranges. The present study was carried out between 1991 and 1995 using radiotelemetry to study the home-range size and to find out extent of fidelity shown by elephants to their ranges in Nilgiri Biosphere Reserve, southern India.

15.2 Methods

15.2.1 Study Area

Nilgiri Biosphere Reserve (76° 0'E and 77° 15' E and 12° 15' N and 10° 45' N), spread over an area of 5520 km², is situated at the junction of three southern states – Tamil Nadu, Karnataka and Kerala. It has an undulating terrain with an average elevation of 1000 m above MSL. Rivers such as Nugu, Moyar and Bhavani and most of their tributaries are perennial and drain the area. The reserve has a diverse climate due to its varied reliefs and topography. The temperature ranges from 7 °C in December to 37 °C in April and receives rainfall both from the southwest (May to August) and northeast (September to December) monsoons. The mean annual rainfall varies from 600 (in the eastern side) to 2000 mm (in the western side). The dry season is from January to April. Corresponding to the gradient in rainfall, the vegetation varies from southern tropical thorn forest in the east to moist deciduous forest in the west with dry deciduous forest in between the two forest types (Champion and Seth 1968). NBR along with its adjoining natural habitats has remarkable faunal diversity and is well known for supporting the largest population of Asian elephants with an estimated population of 5750 individuals (Project Elephant 2007; Baskaran 2013) and relatively undisturbed. Overgrazing by domestic cattle and fire wood collection are serious problems in the eastern fringes of NBR (Baskaran et al. 2012).

15.2.2 Methods

Data on the ranging behaviour was collected from three clans and two bulls monitoring the movements of five elephants (three adult females from three different clans and two adult males), fitted with conventional (VHF) radio transmitter manufactured by the Telonics Inc., USA. The three collared females were named as Priyanka, Wendy and Hariny, and the clans were also named after the collared females as Privanka Clan, Hariny Clan and Wendy Clan. The adult males were named as Salim Ali and Admiral. The collared elephants were regularly tracked from February 1991 to April 1994, and thereafter data was collected at a lower intensity. An attempt was made to collect a minimum of eight locations per month for each elephant. During the greater part of the study, this minimum sample size was achieved. The only exception was the clan *Wendy* which was tracked only twice a month as the distance involved in reaching the clan was extremely large (> 400 km) round trip from the base camp across the Nilgiri Mountain. The bull, Salim Ali, was tracked until June 1992 when its transmitter stopped functioning. The other bull Admiral was tracked until September 1993 when it was shot dead by a local villager.

The locations of the collared animals were plotted on 1:50,000 scale topographic maps (Survey of India), and the data was analysed using the Spatial Ecology Analysis System (SEAS) software developed by John Carey, Wisconsin University, USA. The home range was estimated using minimum convex polygon (MCP) method (Jennrich and Turner 1969) by pooling the data for each individual for the entire study period. Seasonal range was estimated using the pooled data for all the study animals except for Wendy's clan, which was tracked only twice a month, and consequently the smaller sample sizes do not permit such analysis. Home-range fidelity was determined by calculating the activity centre (defined here as arithmetic mean of all animal locations) for consecutive years and estimated the distance between activity centre in consecutive years in order to know how far the activity centre shifted between years. A similar method was adopted for determining the seasonal range fidelity. To determine whether different areas were used during different seasons, the activity centre for each season in each study year and the distance between activity centres for sequential seasons over the years (i.e. dry 1991 to first wet 1991 to second wet 1991, dry 1992 to first wet 1992 to second wet 1992, etc.) were calculated.

15.2.3 Definitions Used in the Study

The following abbreviations and definitions have been used in the context of elephant social units and legal status of the forest areas in the present study. Clan: A clan is defined as a group of elephants consist of related females, and their offspring from sub-adults, juveniles to calves of both sexes, which associate regularly and show coordinated activity and movement (Moss 1988).

- *Bulls/adult males*: Males leave their natal clan at puberty and mostly lead solitary life with weak social bonds with clans and other males (Douglas-Hamilton and Douglas-Hamilton 1975; Moss 1988; Desai and Johnsingh 1995).
- *Protected areas* (PAs): Forest areas that have been designated as national park or wildlife sanctuaries.
- *National park* (NP): An area designated for wildlife conservation. This area comes under the management of wildlife wing (a part of forest department).
- *Wildlife sanctuary* (WS): An area designated for wildlife conservation, but it enjoys a lower legal status than the NP. This area is also managed by the wildlife wing of the forest department.
- *Reserve forest* (RF): The territorial wing of the forest department manages these forest areas. Wildlife wing has no control over this area. These forests are open to normal forestry operations and not legally designated as wildlife conservation area.
- *Revenue land* (REVF): These include forested and non-forested (agriculture and settlements) lands. A part of the land is privately owned, and the rest is the public land under the revenue department (mostly forested land).

15.3 Results

15.3.1 Location-Area Curve

To determine whether the home ranges of the study animals are defined, the homerange sizes were plotted in a chronological order against time axis (monthly) for each study animal separately (Fig. 15.1a). The area curves attained asymptotic value for *Hariny*, *Priyanka* and *Wendy* indicating that home ranges were defined in the case of clans. Similarly, the area curve in the case of the bull *Admiral* also shows asymptotic value (Fig. 15.1b). However, as males during *musth* period have much larger home range than non-*musth* (Desai and Johnsingh 1995), the home range has not been defined in this bull, as this bull did not come into *musth*. Area curve in the case of *Salim Ali* is yet to stabilize (Fig. 15.1b), suggesting that the home range is not defined for this bull also.

15.3.2 Home-Range Size

The clan *Hariny* had the smallest home range of 562 km² (Table 15.1). In contrast, the clan *Wendy* ranged over the largest area of 800 km². The home range of clan *Wendy* included vast inaccessible areas of steep hills, human settlements and cultivated lands. Including these inaccessible areas, the home-range size was estimated to be 1665 km². As the entire area was not accessible, the actual area available to the clan was only 800 km². An intermediate home-range size of 670 km² was recorded for the clan *Priyanka*. The mean home range of the clans was 677 ± 69 km². Among the bulls, *Salim Ali* ranged over a larger area of 375 km², but the other bull *Admiral*

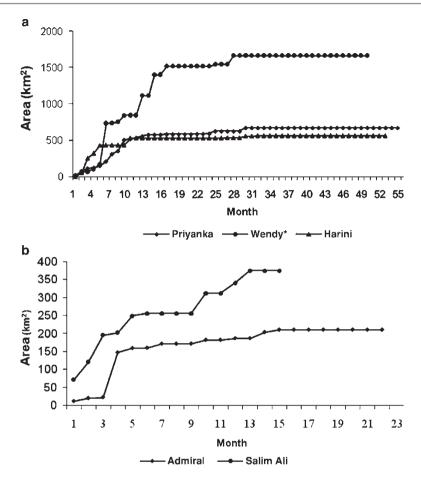


Fig. 15.1 Cumulative monthly increase in home-range size of Asian elephant clan (**a**) and bull (**b**) in Nilgiri Biosphere Reserve, southern India

Table 15.1 Home-range size of elephant clan and bull in Nilgiri Biosphere Reserve, southern

 India, estimated using minimum convex polygon method

Elephant ID		Duration of tracking (month)	# of locations (<i>n</i>)	Home-range size (km ²)
Hariny	(Clan)	47	574	562
Priyanka	(Clan)	52	578	670
Wendy	(Clan)	48	131	800
Admiral	(Bull)	23	257	211
Salim Ali	(Bull)	17	114	375

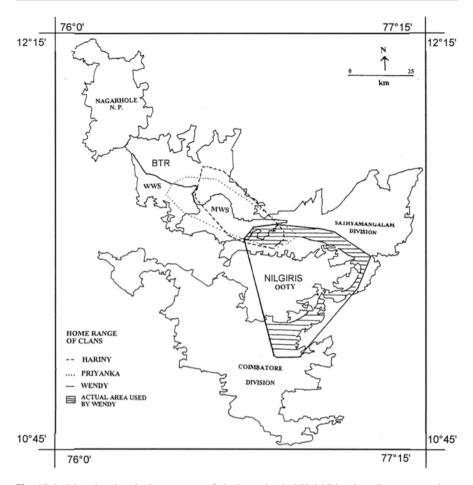


Fig. 15.2 Map showing the home range of elephant clan in Nilgiri Biosphere Reserve, southern India

occupied a very small home range of 211 km². The mean home range of bulls was 293 ± 82 km². It is very important to note that *Hariny* and *Priyanka* mainly ranged in the central part of the protected areas (Bandipur Tiger Reserve, Wynad Wildlife Sanctuary and Mudumalai Wildlife Sanctuary) (Fig. 15.2), which constituted 87% and 84% of *Hariny's* and *Priyanka's* home ranges, respectively. The rest of the clans' ranges consisted of reserve and revenue forests. On the other hand, *Wendy* clan ranged mainly in the dry thorn forests habitats of reserve and revenue forests that constituted 96% of its home range, while the rest was in the protected areas of Mudumalai Wildlife Sanctuary. Data collected before the radio-collaring of this clan also suggests a similar trend of ranging pattern. However, the *Wendy* clan shifted its original range by the second year. Its original range, 96% of which consisted of dry thorn forests habitat of the reserve and revenue forests, was getting highly degraded, and some parts of its range were lost for agriculture and human

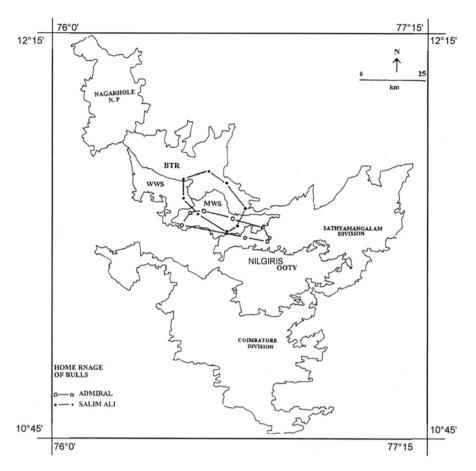


Fig. 15.3 Map showing the home range of elephant bull in Nilgiri Biosphere Reserve, southern India

settlements. In addition, its dry season range along the Bhavani River and Reservoir was also exposed to biotic pressure and habitat loss. Access to the river was mostly cut off by agricultural operations, making a large part of its summer range devoid of water. It is possible that this clan could not sustain itself in the original range, and thus it was forced to shift its range during the second year of this study to a new area towards southwest of the original range, where the elephant density appeared to be much lower than its original range.

A major part (99.7%) of the bull *Salim Ali's* home range was within the protected areas, only a fraction (0.3%) falling within the revenue forests (Fig. 15.3). The other bull *Admiral* had 76% of its home range within the protected areas (Mudumalai Wildlife Sanctuary) and the rest in revenue forests (15%) and reserve forests (9%). The bull *Salim Ali*, a young adult (18–20 year old), did not come into regular *musth* during the study period. The other bull, *Admiral*, a large adult male, also did not

come into *musth*, possibly because of loss of condition from gunshot injuries it had received. The estimated home ranges of both the bulls therefore may represent only their non-*musth* ranges. Desai and Johnsingh (1995) reported that males, during the *musth* period, range over greater areas than when they are not in *musth*. Hence, the present home-range size of the bulls without *musth* range has been taken only as their minimum range. The clan *Wendy* and bull *Admiral* that had considerable part of their range in the reserve and revenue forests (degraded habitats) raided crops, and both elephants were shot by the villagers during the study period. These results suggest that elephant clans and bulls that lost part of their range to agriculture and with the remaining range being extensively degraded may end up in conflict with humans.

15.3.3 Seasonal Range Size

Both the clans ranged extensively and used major part of their home range during second wet season (Table 15.2). Unlike clans, bulls ranged extensively and used large part of their home ranges during the dry season compared to the wet seasons. Patterns of range sizes in different seasons were not uniform among the clans and bulls. For example, *Hariny* clan had the smallest range (216 km²) during the first wet season unlike the *Priyanka* clan that had smallest range during dry season (288 km²). Seasonal movement of elephants from the dry season ranges to first wet season ranges (towards western side) at the end of dry or the beginning of the first wet season and from there towards eastern side by second wet season coincided with the onset of southwest and northeast monsoons, respectively. In turn, from the second wet season range, they returned to the dry season ranges almost at the beginning of the dry season. The above results show that the seasonal range size varies within individual clans and bulls between seasons and between individual clans and bulls in any given season.

15.3.4 Home-Range Fidelity

Home-range fidelity analysis was done for two clans (*Hariny* and *Priyanka*) and a bull (*Admiral*). In the case of clan *Wendy* and bull *Salim Ali*, due to inadequate data for home-range analysis in different years, the activity centre was not calculated.

Table 15.2Seasonal home range of elephant clan and bull in Nilgiri Biosphere Reserve, southernIndia, estimated by minimum convex polygon method

	Seasonal home ra	Seasonal home range (km ²)				
Elephant ID	Dry season	First wet season	Second wet season			
Hariny	328	216	511			
Priyanka	288	420	457			
Admiral	184	72	137			
Salim Ali	277	238	115			

In the case of *Hariny*, the shift in activity centre was 0.4 km between the first and the second year, 1.9 km between the second and the third year and 2.4 km between the third and the fourth year. The overall mean shift in activity centre was 1.6 ± 0.6 km, and the area enclosed by four activity centres was 0.9 km², which is just 0.16% of the home range defined for this clan. In *Priyanka*, the shift in activity centre was 3.8 km from the first to the second year, 6.4 km from the second year to the third year and 5.3 km from the third year to the fourth year, and the overall mean distance was 5.2 ± 0.75 km. The area enclosed by these four activity centres was 13.4 km^2 that is just 2% of the home range defined for this clan. For the bull *Admiral*, the activity centre was calculated for 2 years, and the distance between these 2 years was 6.6 km. As only two points were available, the area enclosed could not be calculated. The small shift between the activity centres of different years and the small enclosed area of activity centres suggest that same area being used over the years, indicative of very strong fidelity shown by the clans and bull to their home ranges.

15.3.5 Seasonal Range Fidelity

To know whether clans and bulls have distinct seasonal ranges, the activity centre year-wise for each season and the distance between activity centres for sequential seasons were calculated over the years. It can be inferred from the results that clan *Hariny* differs from *Priyanka* in having dry and first wet season ranges closest (Table 15.3), while in the latter clan, the two ranges that were closest were dry and second wet. This indicates differences between the clans in their strategy of space use. Similarly, bulls also adopted different strategy of space use (Table 15.3). Such difference in space use pattern among clans and bulls may be a strategy of spacing

Elephant ID	Season	1991	1992	1993	1994	Mean
Hariny	Dry-first wet	_	1.3	0.6	_	0.95
	First wet-second wet	6.4	4.7	4.03	-	5.04
	Second wet-dry	6.2	2.6	1.4	-	3.40
Priyanka	Dry-first wet	7.3	15.6	18.9	-	13.9
	First wet-second wet	14.6	21.6	21.4	-	19.2
	Second wet-dry	-	4.9	1.4	2.6	2.97
Admiral	Dry-first wet	-	11.17	21.4	-	16.43
	First wet-second wet	-	15.73	-	-	15.73
	Second wet-dry	9.47	4.48	-	-	6.9
Salim Ali	Dry-first wet	9.49	-	-	-	9.49
	First wet-second wet	1.10	-	-	-	1.10
	Second wet-dry	11.72	-	-	-	11.72

Table 15.3 Shift in activity centre (km) between consequent seasons arrived plotting core area of each season and estimating the distance between two consequent seasons to understand whether different area used in different season

Elephant ID	Season	Distance between activity centres (km)	Mean distance between/among activity centre (km)	
Hariny	Dry 92–dry 93	1.3	1.8	
	Dry 93–dry 94	2.3		
	First wet 91–first wet 92			
	First wet 92-first wet 93	2.2	_	
	Second wet 91-second wet 92			
	Second wet 92-second wet 93	1.6	_	
Priyanka	Dry 91-dry 92	5.4	4.57	
	Dry 92–dry 93	5.9		
	Dry 93-dry 94	2.4	_	
	First wet 91-first wet 92	2.9	2.75	
	First wet 92-first wet 93	2.6		
	Second wet 91-second wet 92	4.9	3.8	
	Second wet 92-second wet 93	2.7		
Admiral	Dry 92-dry 93	9.09	9.09	
	First wet 92–First wet 93	1.29	1.29	
	Second wet 91-second wet 92	4.85	4.85	
Salim Ali	Dry 91-dry 92	3.0	3.0	

Table 15.4 Shift in activity centre between/among years in the same season to understand whether same area used in every season (range fidelity)

among the range overlapping species to reduce conflicts. To know whether individuals show fidelity to their seasonal ranges, activity centre of the same season between years (dry 1991 to dry 1992, dry 1992 to dry 1993, dry 1993 to dry 1994, etc.) and distance between activity centres were calculated. A comparison of mean distance of activity centres of different seasons with that of the same season among years shows that shift was more between seasons (Table 15.3) than in the same season of different years for all the clans and bulls (Table 15.4). These findings indicate that clans and bulls had different seasonal ranges but used specific areas every year in the same season with strong fidelity to seasonal ranges.

15.3.6 Home Range Overlap

An extensive spatial overlap in the home range was observed among clans and between bulls and among clans and bulls (Table 15.5). A total of 466 km² was used by both *Priyanka* and *Hariny* clans that formed nearly 83% of the *Hariny* clan's range and 70% of the *Priyanka* clan's range, indicating that the *Priyanka* clan had a large area not overlapped by the *Hariny* clan. It may be noted here that the 466 km² area is common to both the clans and thus both had access to space and resources available within. The home range of the clan *Wendy* did not overlap much with the other two clans (though not calculated) as this clan ranged at the periphery of the ranges of the other two clans. Among the bulls, 31% of the home

Elephant ID	Hariny	Priyanka	Admiral	Salim Ali
Hariny	-	83.1	21.8	52.1
Priyanka	69.6	-	20.3	53.8
Admiral	58.2	64.6	-	30.8
Salim Ali	78.3	96.2	17.3	-

Table 15.5 Percentage of home range overlap between elephant clan and bull in Nilgiri Biosphere

 Reserve, Sothern India
 Percentage

range of the *Admiral* overlapped with that of *Salim Ali*, and only 17.3% was vice versa, with a common area of 65 km² available to both the bulls. The percentage range overlap between bulls was, thus, smaller than the overlap recorded between clans. The range of the bull *Salim Ali* overlapped the clan's ranges much more than that of *Admiral*.

15.3.7 Seasonal Range Overlap and Spacing

Overall, the seasonal range overlap between clans and among clans and bulls was highest during the dry and second wet seasons as compared to the first wet season (Table 15.6). There was no overlap between the bulls in any season, as *Admiral* did not intensively use the central part of its range (where its annual range overlapped with *Salim Ali*), and therefore this area was not part of any seasonal range estimated, using harmonic mean distance method with 75% of locations. The area of 466 km² available commonly to both the clans was used mainly during the dry and second wet seasons as shown by the highest overlap in these two seasons. These results clearly suggest that these two clans overlapped in space during all the seasons but more significantly during dry and second wet seasons.

15.3.8 Interclan Encounter

Despite the fact that *Priyanka* and *Hariny* clans overlapped extensively in space maximum to the tune of 100% (*Hariny* clan's range by *Priyanka*) during dry season and 55% during second wet season (*Hariny* clan's range by *Priyanka*), the number of times the two clans observed together or in the vicinity of each other was on only one occasion during the 4 years of observations. The interclan encounter was observed in the feeding ground, in which a large female from the *Priyanka* clan, that was operating more than 100 m away from the *Hariny* clan, moved with raised head and extended ears towards the *Hariny* clan, preventing the feeding of an adult female belonging to *Hariny* clan, by jabbing with her tushes and by depriving the food from the same clump of browse. The adult female of *Hariny* clan crouched herself and consequently moved away from that place with her clan members without any resistance. The next day, the *Hariny* clan showed a displacement of more than 5 km from the encounter spot, while the *Priyanka* clan continued operating

	Range overlap (%)					
Elephant ID	Hariny	Priyanka	Admiral	Salim Ali		
Dry season						
Hariny	-	100	0	100		
Priyanka	13.8	-	37.4	43.1		
Admiral	0	75.1	-	0		
Salim Ali	14	43.6	0	-		
First wet season						
Hariny	-	47.7	0	0		
Priyanka	8.8	-	2.9	19.8		
Admiral	0	19.6	-	0		
Salim Ali	0	37.1	0	_		
Second wet sease	on	· · · · · · · · · · · · · · · · · · ·				
Hariny	-	54.6	14	0		
Priyanka	40.3	-	13.2	0		
Admiral	78.2	100	-	0		
Salim Ali	0	0	0	-		

Table 15.6 Percentage of seasonal range overlap between elephant clan and bull in Nilgiri
 Biosphere Reserve, Southern India

close to the same area. The results on range overlap and the observations on interclan encounter suggest that despite extensive spatial overlap, clans mostly avoided each other and there appears to be aggression and hierarchy among them when they rarely encounter with each other.

15.4 Discussion

Within the species, the home range varies widely between areas and within the area and between the sexes and individuals. These variations have been attributed to different factors. Variations in the home-range size of elephants have been related to habitat quality, both in Asia and Africa. Olivier (1978) and Easa (1988) found the home ranges of the Asian elephants to be larger in the primary forest and smaller in secondary forest. In Africa, the smaller home ranges of elephants have been related to higher rainfall (Leuthold 1977; Thouless 1996) and better habitat quality (Douglas-Hamilton 1972). In the present study, the clans had home-range sizes that varied from 562 to 800 km² with a mean size of 677 km². The home-range size of the Wendy clan (800 km²) was much larger than the one estimated for the Hariny and Priyanka clans. The major part (96%) of the Wendy clan's range was outside the protected area, a rain shadow area mainly dry thorn forests, which was subjected to high biotic pressure. The availability of grass biomass was very low in dry thorn forests when compared to dry deciduous forest (Baskaran 1998; Baskaran et al. 2010). Thus, the larger range of clan Wendy could possibly be ascribed to low rainfall, poor quality of the habitat and consequently limited food supply. The home-range size estimated for the three clans in the present study was larger than reported earlier studies in this region (Sukumar 1989; Desai 1991), other parts of India (Easa 1988; Joshua and Johnsingh 1995) and other parts of Asia (Olivier 1978). The small range sizes estimated by the earlier Asian studies could be either due to smaller sample size (re-sightings) resulting in underestimation of home range or due to compression of original range due to developmental activities and biotic pressure as reported in Asia (Joshua and Johnsingh 1995) or physical barriers as reported in Africa (Douglas-Hamilton 1972; Dunham 1986).

Home ranges estimated for bulls in the present study represented only non-musth range. Bulls, during musth period, are said to move extensively in search of oestrous females (Barnes 1982; Desai and Johnsingh 1995; Joshua and Johnsingh 1995). Therefore, the present home range of bulls without the *musth* range could be treated as the minimum range size for bulls. Though, in the present study, the home ranges of bulls could not be defined completely, it was still larger compared to earlier studies in Asia (Olivier 1978; Sukumar 1989; Desai 1991; Joshua and Johnsingh 1995). Bulls being solitary animals are expected to range shorter than clans as speculated by Olivier (1978) as food requirements of a solitary individual per unit time is lesser compared to clans. However, for adult males in polygynous species especially during the reproductive period, oestrous females are the most important resources that are scarcely available. Males might enhance the probability and frequency of encountering potential mates and hence increase their reproductive success by enlarging their home range (Lindstedt et al. 1986). Thus, the need for locating oestrous females, a resource scarcely available in a given breeding period, imposes on the bulls to cover equal or a much larger ranges than clans. Therefore, bulls may have equal or much larger ranges than clan as shown by other studies in Asia (Daniel et al. 1995; Joshua and Johnsingh 1995) and Africa (Leuthold and Sale 1973; Leuthold 1977; Viljoen 1989a).

Seasonal home ranges estimated for the clans Hariny and Priyanka were generally larger during the wet season than in the dry season. The trends of seasonal range size recorded in the present findings are consistent with earlier studies in Asia (Easa 1988; Daniel et al. 1995) and Africa (Leuthold 1977; Viljoen 1989a; De Villiers and Kok 1997). The dry season ranges of elephants in Nilgiri Biosphere Reserve were restricted to areas along the perennial water sources, since the temporary water sources dry up during summer. Therefore, the relatively small dry season ranges of the clans could be attributed to restricted availability of water. Desai and Baskaran (1996) found that the clans Hariny and Priyanka significantly preferred areas close to water. Movements of elephants in Africa also indicated a sedentary nature in dry season, followed by dispersal and scattering during rains (Rodgers and Elder 1977; Jachmann 1988). During dry season, apart from restricted water availability, food quality and quantity also are very low compared to wet season. It would be better choice for elephants to restrict themselves along the perennial water sources and exploit whatever food resources that are available by spending little energy, instead of spending much of its limited energy by moving widely in searching good quality food and commuting to get water as speculated by Jachmann (1988). In Nilgiri Biosphere Reserve, in contrast to clans, bulls exhibited larger ranges during dry season. The reason for this might be that both the bulls used extreme ends of their

annual ranges during the dry season. The central part of home range was used mostly for travelling between second wet and dry season ranges with relatively scattered use. During this period, they were also found to use small streams with very limited water supply relatively for longer period than the clans did. Bulls being alone can afford to withstand low water availability and sometimes even do without it unlike the females that cannot do the same as they live in larger groups and with dependent calves. Therefore, water availability may not be influencing bull's movement as much as it does clan's movement in the study area.

Apart from water, the other factor that influenced the dry season movement of elephants in the study area was forest fire which used to be very severe in the deciduous forest once in every 4 or 5 years due to very high accumulation of litter biomass from tall grass and with teak leaf fall. In years of severe forest fires, elephants during the dry season moved to their second wet season ranges and remained until mid-dry season as forest fire wipes off all the food resources available at the ground level. During wet season, rainfall influenced the movements of elephants by providing many temporary water sources and by favouring a luxurious growth of grass. Generally, the seasonal movement of elephants from the first wet season to second wet season range took place during the beginning or mid-October, and elephants remained in the second wet season ranges until the beginning of dry season. Unusually, in years when there was delay in the onset of second monsoon, elephants returned within a few days from their second wet season range to the first wet season range and waited for 2–3 weeks until the onset of monsoon and fresh growth of grass. However, such movements were restricted within the individual home range of the clans and bulls, and no wandering took place outside the home range due to rainfall. These findings clearly reveal the magnitude of rainfall influence on the wet season movements of elephants.

All the study animals (except Wendy) presently showed strong fidelity to their home ranges, a phenomenon recorded earlier by Baskaran and Desai (1996) and Baskaran (1998) in Asian elephants and Viljoen (1989a) in African elephants. In tropical forest, resource distribution and abundance vary within a habitat between seasons and thus within the home range too if home range lies in different habitats. It implies that the entire home range would not be always uniform regarding resource distribution and abundance. Parts of the home range would be with abundant resources at different times of the year depending on the season. This would mean that elephants use different parts of their home range during different seasons depending on changes in resource availability. Resources in a given habitat do not normally change between years. Therefore, the seasonal range would also remain stable, unless disturbed by drastic changes. If a long-lived species like elephant confines its movements within a small area (home range) and uses this area year after year, it could acquire knowledge about the resource distribution and abundance that vary spatially and temporally, especially in a heterogeneous habitat. Such knowledge about the resource distribution and abundance would certainly help to optimize their resource use and therefore enhance their reproductive success. But if the individual or group keeps shifting the home range from year to year, any familiarity gained in the previous year would be of little or no use in the new area. This

means that the use of resources may be largely a matter of chance, which is not the best way of resource use for a long-lived species. As mentioned earlier, for an optimum use strategy to use the same home range repeatedly over the years and particular area (within the home range) every year during the same season, elephants should have strong fidelity to their home range and seasonal ranges. Thus, fidelity shown by elephants to their ranges could be a strategy adopted for optimal use of resources.

15.4.1 Range Overlap and Spacing

Home ranges of the clans Hariny and Priyanka overlapped each other, but the home range of the clan Wendy did not overlap much, as its range was near the periphery of the ranges of the other two clans. Similarly, little overlap of the home range between bulls in the present study could also be due to the fact that these bulls were basically from two different areas. The bulls' ranges overlapped little with those of clans in the present study, probably because of the absence of *musth* range in males. The breeding bulls have a strategy to build up the body condition during the nonmusth time with limited movements resulting smaller non-musth range and range widely during *musth* period, in search of oestrous females (Joshua and Johnsingh 1995). It is obvious that overlap in home ranges among clans and between clans and bulls is more, and the degree of overlap varies widely depending on the location of home ranges. That is a clan or bull will overlap more with another clan or bull whose home range exists in the same area rather than with that of another clan or bull at the periphery of its home range. The degree of overlap may also be a function of elephant density and availability of resources as suggested in deer by Baker (1978). The overlap of home ranges is also determined by the spacing of essential resources most restricted in their distribution (Altman 1974).

The seasonal range overlap between the clans was more during the dry season followed by the second wet season and far less during the first wet season. A similar pattern of overlap was also observed between the clans and bulls. The limited availability of perennial water sources and the restriction of elephant movements around them during dry season could be the reason for greater overlap in the dry season range among the study animals. On the other hand, in the wet seasons, as elephants disperse over the temporary water areas, there was less overlap. The present finding of high overlap between clans in the dry season range differs from the findings of McKay (1990) who stated that home ranges of herds tended to overlap more extensively during the rainy season than during dry season in the Gal Oya National Park, Sri Lanka. Bull's seasonal ranges did not overlap each other in any season as they were basically from different areas. Joshua and Johnsingh (1995) estimated the seasonal range overlap between clan and bull and showed that the overlap was high during winter (14 km²) compared to summer (9 km²) and monsoon (7 km²), being attributed to the *musth* period of the bull.

Although, the differences in the sizes of seasonal ranges of bulls can be due to variations in the habitat quality and environmental conditions of their ranges, differences between the clans may not be so because the spatial distribution and extensive overlap of home ranges of *Hariny* and *Priyanka* showed that these two clans operated in the same area. These two clans, with almost the same herd size, had an overlapping area of 466 km² which was used by them mostly in the same season. Hence, it can be reasonably expected that the two clans have a similar range use pattern as environmental factors in an area act on all the clans uniformly. However, the findings show that these two clans show more variations in seasonal range sizes and in overlap (within clan between seasons), which could be as a result of hierarchy and spacing. It has been suggested that in mammals, females are concerned with obtaining food while males compete for mates (Greenwood 1980, 1983; Dobson 1982). There were many occasions in which non-collared adult bulls were observed to feed within the vicinity of the bull Admiral, when males were not in musth. During the course of observation, no competition between bulls for a mate was observed, as the breeding bulls were extremely low in the population. However, Eisenberg et al. (1971), McKay (1990) and Desai (per. comm.) observed competition between bulls for mates. The observed tolerance among bulls in the feeding grounds may not be true when it comes to mating requirements.

The present study has answered, how a given space may be used by individuals of two different clans (*Hariny* and *Priyanka*), whose range overlap extensively. The spatial distribution of home range and its percentage overlap among the two clans *Hariny* and *Priyanka* suggest that these clans were sharing the same space within the population range. Both the clans, in the same season, used an overlapping area of 466 km² that constituted 83% and 70% home ranges of former and latter clans, respectively. However, these two clans were observed to encounter each other only once during the study period, and such observations suggest that normally, the clans space out themselves and mostly avoid each other, despite extensive spatial overlap. A recent study (De Villiers and Kok 1997) on African elephants observed such avoidance behaviour between females in core areas.

15.4.2 Determinants and Consequences of Interclan Encounter

Spacing has often been discussed in the context of resource defence in different animals (Zahavi 1971; Gill and Wolf 1975; Carpenter and MacMillen 1976; Simon and Middendorf 1976). Temporal partitioning of overlapping territories as a strategy to avoid interference competition has been documented for a lizard population (Simon and Middendorf 1976). Encounters among neighbours with extensive range overlap, which resulted in spacing, have been documented in some animals like chipmunks (Getty 1981). Among Asian elephants, the behaviour observed in the interclan encounter (*Hariny* and *Priyanka*) in a feeding ground suggested the existence of hierarchy and resource defence among clans. In the present study area, Desai (per. comm.) also had observed resource defence by clans and subtle aggression when two clans met at common water holes and feeding grounds. Studies on the behaviour of African elephants (Laws and Parker 1968; Laws 1969) suggest that territorial mechanism may operate at family or clan level. Douglas-Hamilton (1972)

stated that, in competitive situations, attacks do occur, and such attacks may be within the family units, between family units of the same kin group or between apparently unrelated groups. If the resource is distributed unpredictably both in space and time, defence may be a costly strategy because there is no guarantee that a defended patch can provide sufficient resources. But defending a resource which is within the vicinity is not as costly as defending an entire range. For mammals, to defend foraging areas may be costly (Brown and Orians 1970). So elephant clans possibly defend resources within their immediate vicinity. The agonistic behaviour of dominant clan over the subdominant for the resource could be an important reason for encounter avoidance.

Many studies often cite the avoidance of agonistic encounters as the main factor promoting spacing (Recher and Recher 1969; King 1973; Tingay 1974; Young 1989). So clans space them self in such a way that they will not use a given space at the same time. This means a given space or patch can only be used by one clan at one time. So the overlapping clans in a population seem to use a given space on a rotational basis, based on their hierarchical position in the population, with dominant clan using a patch in optimal time and subdominant one in suboptimal time as shown by Baskaran (1998). Such a hierarchy and spacing among the overlapping clans also influence the seasonal habitat use pattern, resulting in dominant clans having prior access to good quality habitat and food (Baskaran 1998), thereby show better survival and reproductive success.

15.5 Management Recommendations

Small patches of revenue lands exist in Sigur and Singara Reserve Forests and these are encroached upon gradually, as clans and bulls show strong fidelity to their annual and seasonal ranges; further loss in habitats would increase human–elephant conflict. Therefore, the unoccupied revenue lands within the forest areas should be transferred from the revenue department as part of the Mudumalai Wildlife Sanctuary. The habitat in Nilgiri Biosphere Reserve is considered an optimal one for elephants in the whole of Asia. When elephant clans show a mean home range of over 600 km² in this optimal habitat, any other elephant reserve less than this size (600 km²) may not therefore be viable. As overlap between clans varied from 30% to 100% (Desai et al. unpublished data), a minimum area of 900 km² is essential to provide sufficient space for overlapping clans. Therefore, elephant reserves less than this size should be enlarged wherever possible.

Water is the major limiting factor for elephants during the dry season. Elephants concentrate around perennial water sources in all the habitats during the dry season. At present, there are many places (viz. Doddakatti, Imparhallah and Onnaretty in Mudumalai Wildlife Sanctuary and Chemmanallah and Maddur in Bandipur Tiger Reserve), which are without perennial water sources. Creating water holes in these areas will help to spread out the elephant distribution in the dry season. Ben-Shahar 1993 reported that elephants in Africa cause more impact on vegetation around perennial water source than away from it. Studies in Africa and Asia clearly show

that elephants concentrate around perennial water areas during the dry season. Therefore, providing more water sources in areas, where it is lacking, would reduce the dry season impact of elephant on vegetation.

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