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ORIGINAL ARTICLE

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Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus)*

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Abstract We report on the genetic evaluation and behavioral study of social organization in the Asian elephant (*Elephas maximus*). Although Asian elephants and African elephants (*Loxodonta africana*) were previously thought to have similar social organizations, our results demonstrate a substantial difference in the complexity and structure of Asian elephant social groupings from that described for African savanna elephants. Photographic cataloging of individuals, radio telemetry, and behavioral observations in Ruhuna National Park, Sri Lanka, enabled us to assign associated females and young to four groups with overlapping ranges. Genetic sampling of individuals from the four groups in Ruhuna National Park and three other groups in surrounding areas, conducted through PCR amplification and sequencing of mitochondrial DNA from dung, supported the matriarchal nature of female groups and the lack of inter-group transfer of females. Behaviorally and genetically, the identified social groups were best described as "family groups". We did not find any evidence for the existence of social groups of higher complexity than family groups.

Communicated by S. Boinski

This paper is dedicated to the memory of G.V. Gunawardene, for invaluable assistance and many enjoyable hours of companionship in the field. He was killed by an elephant he was trying to save, in the line of duty as a game guard at the Department of Wildlife Conservation, Sri Lanka.

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Introduction

Kinship is a central tenet in the evolution of sociality, and the elucidation of relatedness between interacting individuals is a key variable in understanding social organization and its evolution (Hamilton 1964; Pamilo et al. 1997). While humans have achieved a complexity of social organization far greater than other species, non-human mammals exhibit levels of social complexity greater than other vertebrates (Wilson 1975). Elephants, primates and cetaceans are considered to have independently evolved peaks in brain size and, concomitantly, peaks of social complexity among mammals (Connor et al. 1998; Wilson 1975). Elephant social organization reportedly consists of relationships that radiate through a multi-tiered network encompassing whole populations, and is considered comparable to that of non-human social primates in complexity (Moss and Poole 1983; Wilson 1975). Knowledge of elephant socio-biology is largely based on a few long-term studies of African savanna elephants (*Loxodonta africana africana*), which occupy a fundamentally different habitat to the forest-living Asian elephant (*Elephas maximus*). Study of similar organisms occupying different ecological contexts can aid in the understanding of ecological determinants of social organization and its evolution. In the present study, we describe the social organization of Asian elephants in southern Sri Lanka and discuss the possible causation of observed differences from that of African savanna elephants.

While no previous studies have specifically investigated the social organization of Asian elephants, both Asian and African elephants are thought to have an identical, or largely similar, sexually dimorphic social organization (Eltringham 1982; Lee 1991; Sukumar 1989, 1994). In both species, females and young are thought to form a matriarchal society organized as a multi-tiered

hierarchy of mother-calf units, families, kinship groups, clans, and subpopulations (Douglas-Hamilton 1973; Lee 1991; Moss and Poole 1983). Males are thought to disperse on reaching adulthood and to be essentially solitary thereafter (Douglas-Hamilton 1973; Moss and Poole 1983; Sukumar 1994). This study reports the first genetic evaluation of social structure in either elephant species.

Units of social organization

As no definitions of social groupings specific to Asian elephants are available in the published literature and both species are thought to have a similar social structure, we base our hypotheses of Asian elephant social structure on that described for African elephants. The accepted social hierarchy among female elephants is defined mainly on behavioral characteristics based on an underlying hierarchy of relatedness, on the implicit assumption that extent of association and relatedness are correlated.

Although mother-calf dyads and triads form the basic units of association, the "family group" is the basic level of social organization among females. A family group is led by a "matriarch", and may include a number of generations of her offspring. (Eltringham 1982; Wilson 1975). Family members are closely associated, spending 70–90% of their time together (Lee 1991). Family groups of African elephants are reported to consist of up to 10–20 females and their offspring (Wilson 1975), and to average 9.4 individuals in Amboseli, 7.8–12.3 in East Africa, 10 in Lake Manyara, and 6.3 in western Uganda (Eltringham 1982).

Fission of a family group, precipitated by a factor such as the death of a matriarch, gives rise to daughter groups that continue to associate with each other, forming a more complex social grouping termed a "kinship group" (Douglas-Hamilton 1973; Eltringham 1982; Wilson 1975). Behaviorally, a kinship group is defined as two or more family groups which spend 35–70% of time together (Lee 1991).

Population growth over time leads to the multiplication of kinship groups, which together form large social complexes, giving rise to a third level of organization termed a "clan" (Douglas-Hamilton 1973; Eltringham 1982; Moss and Poole 1983; Wilson 1975). A clan may consist of 50–250 individuals (Lee 1991), and is defined as a collection of kinship groups that share the same geographic range (Moss and Poole 1983). A fourth level of organization termed a "subpopulation", consisting of clans living in a shared geographic area, has also been suggested (Lee 1991; Moss and Poole 1983).

Study objectives

Elephants have a life span of almost 60 years. Thus, even with decades of observational study, relationships beyond filial and sibling have remained largely conjectural (Eltringham 1982) and hypotheses concerning elephant sociobiology have gone untested for many years. In contrast to observational methods, recent advances in molecular techniques enable "instantaneous" estimation of relatedness between individuals.

The clonal and strictly maternal inheritance of mitochondrial DNA (mtDNA) in mammals (Avise 1994) enables lineage tracing of matriarchal social groupings. In the present study, we follow this approach, using mtDNA to distinguish matrilines in behaviorally identified social groupings.

Acquisition of tissues for genetic analysis from free-ranging Asian elephants poses many obstacles, due to their endangered status and the logistics involved. The use of dung as a source of DNA or "molecular scatology" (Gerloff et al. 1995; Hoss et al. 1992; Kohn et al. 1995) eliminates many sampling constraints (Kohn and Wayne 1997), and we have had much success in its application to Asian elephants (Fernando et al., 2000). Here we report on the first use of genetic analysis to the study of social behavior in elephants, using molecular scatology, behavioral observations, and radio telemetry to test hypotheses on the social organization of Asian elephants.

We investigate whether Asian elephants have an identical social structure to African savanna elephants by using behavioral observations and radio telemetry: specifically, that the observed patterns of association and genetic structure of social groupings observed in Asian elephants correspond to those defined for African elephants. Through genetic sampling of female groups, we test the hypothesis that behaviorally identified social groups have an underlying matriarchal genetic structure: specifically, that the distribution of mitochondrial haplotypes within social groups is compatible with descent of group members from a single foundress within a time frame relevant to observed social organization.

Methods

Study sites

The main study site, Ruhuna National Park (RNP) is located in the southeast of Sri Lanka (6 15′–6 35′N; 81 15′–81 35′E), and two additional sites, Uda Walawe National Park (UWNP), and Mirrijjawila lie approximately 30 km to the west and southwest of RNP, respectively (Fig. 1). RNP consists mostly of low-visibility scrub forest with a few clearings, while UWNP contains more savanna-type grassland, and an area of tall forest. Mirrijjawila is not a conservation area and consists of scrub forest interspersed with human habitations. The behavioral study was conducted in RNP, while genetic sampling was carried out in all three areas. As formerly contiguous elephant habitat, development activity over the past two decades has led to a decrease in connectivity of the three study areas. However, movement of elephants between them is still possible.

Behavioral study

Unlike African savanna elephants, Asian elephants inhabit low-visibility habitats, making observation difficult. In RNP, visibility ranged from 3 to 10 m within the dense scrub forest inhabited by

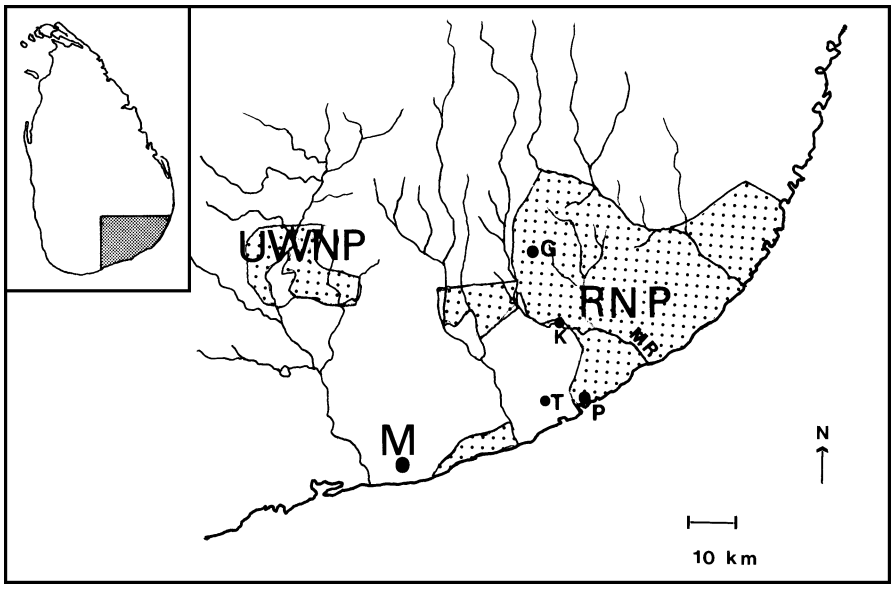

Fig. 1 Map of the study areas (*UWNP* Uda Walawe National Park, *RNP* Ruhuna National Park, *M* Mirrijjawila, *G* Galge, *K* Kataragama, *T* Tissamaharama, *P* Palatupana, *MR* Menik River)

elephants. Scattered short-grass clearings and watering places provided the best opportunities for observing them, and observational data were limited to encounters at such localities. Identification of individuals, and observational study of elephants in the RNP were conducted by us from 1993 to 1996. Individual identification was based on photographic cataloging of individuals and recording of distinguishing characters such as sex, height, ear tears, tail tuft pattern and length, de-pigmentation patterns, and the presence of body lumps. In the present study, the term "female group" is used to denote a cluster of associated females and young, and not to specify any particular social context. An "encounter" with an individual female or female group was recorded when any member or members of an identified group were observed and we were reasonably sure that we had detected all associating individuals present. For observational data, association between individuals was defined as their occurrence at the same point in time within 100 m from each other, considering habitat visibility. For telemetry data, association was defined as a detected distance of less than 1 km between same-day locations of two individuals. The greater distance and time interval adopted for telemetry data was because of the possible error in estimating distances between individuals by this method and the time taken to obtain locations for animals, which would bias results positively. Our study aimed to identify clusters of associating individuals, by using direct observation and radio telemetry.

Radio-collaring of four females (Dhangari, Elsina, Hamine, and Vinitha) and one male was conducted by the Department of Wildlife Conservation, Sri Lanka (Desai 1995). Dhangari and Elsina did not have any dependent offspring at the time of collaring; Hamine had an offspring less than a year old, and Vinitha was in mid-pregnancy (Desai 1995).

We tracked the collared elephants from February 1996 to October 1998. Each animal was located an average of once every 5 days in the 1st year and once a fortnight in subsequent years. Radio telemetric locations were obtained through triangulation, or homing-in on the signal until the animal was visualized. Locations were geo-referenced with a hand-held Sony GPS unit to an accuracy of ±50 m. Home ranges were estimated using the Minimum Convex Polygon method (MCP: Mohr 1947), with exclusion of non-use areas included as an artifact of the MCP method of analysis (White and Garrot 1990). Home-range estimation was based on observations only for one group that did not have a radio-collared female, and on radio telemetry data for the other groups.

Genetic analysis

We elected to analyze sequence from a 600-bp segment of mitochondrial DNA, including the hyper-variable left peripheral domain of the D-loop (Douzery and Randi 1997), which evolves more rapidly than coding regions, providing higher resolution in genetic studies. Mutation accumulation in the analyzed segment of mtDNA in elephants occurs at a rate of ~1% per million years (Fernando et al., 2000). With a generation time of 20 years in elephants, on average a single base change would occur only once every 8333 generations in a 600-bp segment. Thus, polymorphisms in the mtDNA of individuals observed in the present study are unlikely to have arisen within a time frame relevant to social organization, allowing us to consider individuals with different mitochondrial haplotypes to be maternally unrelated. Thus, if all members of a social unit shared a single haplotype, it would support a hypothesis of their descent from a single foundress.

We evaluated statistical evidence in support of the hypothesis that all individuals within a social group share the same mtDNA haplotype as follows. We tested the null hypothesis that genotyped individuals (with sequenced mtDNA haplotype) were randomly associated in social groups, against the alternative hypothesis that all genotyped individuals in a social group share the same mtDNA haplotype. We employed a randomization test in which genotyped individuals were repeatedly randomized among social groups, without changing the number of genotyped individuals in each group and pooling groups with the same mtDNA haplotype. It should be noted that this test does not require that all individuals in each group be genotyped, nor does it require knowledge of the number of ungenotyped individuals in each group.

Sample collection

Approximately 5 g of dung was collected from individual boli and stored in screw-cap tubes at ambient temperature in 95% ethanol. Dung samples were collected from identified individuals in RNP, UWNP, and Mirrijjawila by collection upon observed defecation. Samples for female groups were obtained from 32 individuals of the 4 groups in RNP, 7 individuals of 2 groups in UWNP, and 3 individuals of a single group in Mirrijjawila. We were able to sample all members of a particular group only for one group in YNP, as samples were collected only when they could be unambiguously assigned to individuals (i.e., where particular individuals were observed defecating in open areas during daylight hours, and the group moved away soon after, enabling the collection of the sample without disturbance to the animals or danger to the collector).

DNA extraction, amplification, and sequencing

Approximately 0.5 g of each sample was treated with SDS and Proteinase K and DNA extracted with phenol/chloroform/iso-amyl-alcohol. Extracts were purified using QIAGEN spin columns and the manufacturer's protocol, and stored at –20°C. A 630-bp segment of mtDNA was amplified using primers MDL 3 [5′-CCC-ACAATTAATGGGCCCGGAGCG-3′; based on a mitochondrial sequence from an Asian elephant (C. Wemmer, personal communication)] and MDL 5 [5′-TTACATGAATTGGCAGCCAACCAG-3′; based on a cytochrome b sequence from an African elephant in Irwin et al. 1991]. The first 109 bp of the amplified segment coded for the C terminal of cytochrome b; the next 135 bp coded for threonine and proline tRNAs, and the rest was non-coding mitochondrial control region. PCR amplification was performed in 25-µl reactions using 1 µl DNA extract, 2 µl 100 mg ml^{-1} BSA, 2.5 µl 10× PCR buffer, 2.5 µl 8 mM dNTP mix (Promega, Madison, Wis.), 0.5 µl 10 µM primers, 0.1 µl Taq DNA polymerase (Perkin Elmer Cetus, Emeryville, Calif.), and 15.9 µl water. Reactions, in a Perkin Elmer Cetus programmable DNA Thermocycler, were preceded by a 4-min denaturation step at 95°C followed by 40 cycles of 1 min each at: 63°C annealing, 72°C extension, and 94°C denaturation. Amplifications were electrophoresed on 1% agarose, stained with ethidium bromide, bands visualized under UV and punched out with a pipette tip, melted in 50 µl H_20, and 2 µl used as template for a 50-µl secondary amplification with the same conditions and reactant concentrations. Reamplified PCR products were electrophoresed on 2% low-melt agarose, stained with ethidium bromide, and product bands excised under UV, and purified using QIAGEN spin columns and the manufacturer's protocol.

To guard against contamination, DNA extractions were conducted in a separate room from amplifications, using different sets of equipment. PCR reactions were set up in a UV sterilized hood and negative controls were conducted with every PCR reaction. Negative controls for primary amplifications were punched out inline with the bands for the amplified samples and used as negative controls for secondary amplifications.

Sequencing was carried out at the University of Oregon Sequencing Facility, in an Applied Biosystems ABI 377 automated DNA sequencer using Dye Terminator Cycle Sequencing. Initially, all amplified products were sequenced in the forward direction using primer MDL 5 and each new haplotype identified was sequenced in the reverse direction using primer MDL 3. Of the amplified segment, 600 bp corresponding to bases 15,145–15,753 of human mitochondrial DNA (Arnason et al. 1996) was used in the analysis.

Results

Behavioral study

Observational study and radio telemetry enabled the identification of four female groups in RNP: Yala I, Yala II, Thambarawa, and Katagamuwa. Yala I and II groups were habituated to humans and observable in daytime. The other two groups were extremely wary and usually spent the daytime under cover of scrub forest. The Yala I group consisted of 9 members (5 adult females, 1 subadult female, 3 juveniles), and Yala II of 19 (7 adult females, 1 subadult male, 3 subadult females, 8 juveniles). The Thambarawa group consisted of approximately 24 members (11 adult females and subadults, 13 juveniles), and the Katagamuwa group 7 (4 adult females, 3 juveniles).

Association within groups

The four groups in RNP were observed to consist of all members on 29% of encounters (Table 1). Telemetry data for the females Elsina and Hamine from the same group indicated a lesser association between group members than observational data, with only 18% of same-day locations being less than 1 km apart (Table 2).

Observational data on Dhangari and Elsina, who did not have dependent calves, indicated that they spent considerable time alone, no other group members being observed in 5 out of 17 encounters of Dhangari, and 16 out of 29 encounters of Elsina. Telemetry data of Elsina and Hamine demonstrated that members of a single group could forage up to a few kilometers from each other (Elsina and Hamine – mean distance between same-day telemetric locations 3.99 km, SD 3.33 km, range 0–17.14 km, n=106 paired locations). Therefore, both observational and telemetry data suggested a loose association between members of observed groups.

Table 1 Observational data on association within female groups

Group	No. of encounters	No. of encounters where all members were present
Yala I	24	06
Yala II	14	05
Thambarawa	37	10
Katagamuwa	04	02
Total	79	23

Table 2 Telemetry data on association between radio-tracked females. The group each female belongs to is *in parentheses;* no. of locations within 1 km from each other/no. of paired locations

	Elsina (Thambarawa)	Vinitha (Katagamuwa)	Dhangari (Yala I)
(Thambarawa) Hamine	19/106	1/56	0/28
(Thambarawa) Elsina		0/63	0/28
(Katagamuwa) Vinitha			0/20

Table 3 95% MCP (Minimum Convex Polygon) home-range extents of the four female groups in Ruhuna National Park

Group	Home-range extent (km^2)
Yala I	61.1
Yala II	57.5
Thambarawa	121.2
Katagamuwa	119.5

Association between groups

The radio-tracked females had well-defined and comparatively small home ranges (Table 3) to which they showed high fidelity (data not shown). The home ranges of the four groups were proximal or overlapping (Fig. 2). [The estimated home range of Yala II group (Table 3) is likely to be an underestimate as it was based solely on observational data (Baskaran et al. 1993; Leuthold 1977) and its actual overlap with the other groups is likely to

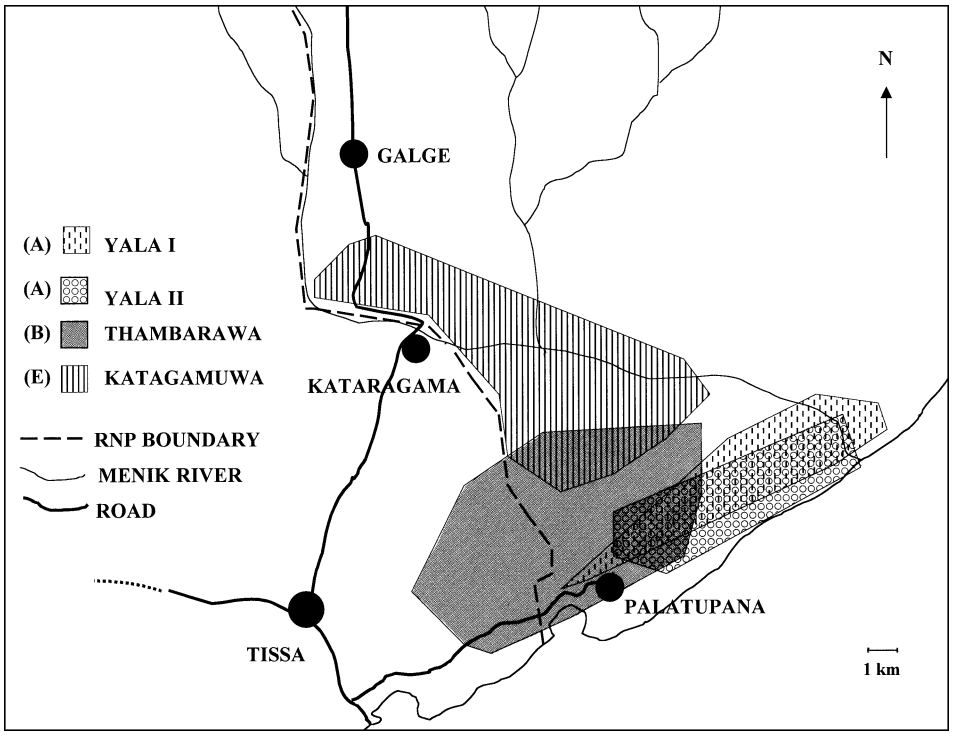

Fig. 2 Home ranges of the four female groups in Ruhuna National Park

be greater than the observed extent.] Observationally, we failed to identify any instances where members of different groups associated with each other. Radio telemetry data showed a single occurrence of a location less than 1 km from each other for Thambarawa and Katagamuwa groups, but none between Thambarawa and Yala I or Katagamuwa and Yala I groups.

Genetic analysis

We were able to obtain target sequence from all analyzed samples. Alignment of the amplified sequences found five mitochondrial haplotypes in the sampled animals (Table 4). No polymorphisms were observed within any female group, all sampled individuals from a single such group sharing the same haplotype. Thus, groups were generally identifiable by their haplotype. Yala I and II groups shared haplotype A, while the Thambarawa and Katagamuwa groups had haplotypes that differed from each other, as well as from Yala I and II (Table 5).

Of the five haplotypes observed among female groups from the three locations, RNP, UWNP, and Mirrijjawila, haplotype E was common to RNP and UWNP while the others were unique to each location (Table 5). On evaluating the statistical evidence in support of the hypothesis that all individuals within a social group share the same mtDNA haplotype, the probability that the data conform as closely as observed to the alternative hypothesis (with all genotyped individuals within each group sharing the same mtDNA haplotype) by chance was:

$$p = \frac{(7+9)!12!(4+4)!3!3!}{(7+9+12+4+4+3+3)!} = 10^{-23}$$

Thus the data in Table 5 provide extremely strong statistical evidence for rejecting the null hypothesis in favor of the alternative hypothesis. This strongly suggests that all individuals within a social group share the same mtDNA haplotype, and because of the matrilineal inheritance of mtDNA, that all individuals in a social group have descended from a single female in the recent past (prior to mutation in the sequenced DNA).

Discussion

We found a single mitochondrial haplotype among all sampled members within each observationally identified group of individuals. Although the presence of unrelated females cannot be conclusively excluded as only one such group was sampled in its entirety, our findings strongly support the hypothesis that all members of such groups are descended from a single foundress. This confirms the matriarchal nature of female social organization in Asian elephants.

Groups with overlapping or adjacent ranges and different haplotypes maintained their maternal genetic identity, supporting the hypotheses that female groups in Asian elephants are closely knit, and there is no inter-group transfer of females (McKay 1973). In many social mammals, such as primates (Brockelman et al. 1998; Hashimoto et al. 1996; Morin et al. 1994), cetaceans (Amos et al. 1993), and large carnivores (Girman et al. 1997; Packer et al. 1991; Pusey and Packer 1987), groups of associating individuals are composed of both sexes, and inter-group transfer of females is not uncommon. The social organization of the white-nosed coati (*Nasua nari-*

Table 4 Polymorphic sites between haplotypes. The numerical position of each polymorphic site is indicated above each position. Base position no. 1 of the analyzed segment corresponds to position no. 15,145 of the human mitochondrial sequence. A *period* denotes a matching base with the topmost sequence

Haplotype	0 1 1	0 1 8	0 6 0	0 7 2	1 5 4	2 1 7	2 4 8	3 8 6	3 9 5	4 0 5	4 0 6	4 1 6	4 1 7	4 2 5	4 3 9	4 4 3	4 5 5	4 5 9	5 3 0	5 6 6
A	T	C	T	C	A	A	C	T	G	C	A	T	G	C	C	T	G	A	T	T
B	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	C	.
D	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E	C	.	C	T	G	G	T	.	A	T	.	C	T	T	T	C	A	.	C	C
F	C	T	.	T	G	G	T	C	A	T	G	C	T	T	T	C	A	.	C	.

Table 5 Distribution of mitochondrial haplotypes within and among female groups

Location	Social group	Mitochondrial haplotype	No. individuals of each haplotype	No. sampled/ no. in group
RNP	Yala I	A	9	9/9
RNP	Yala II	A	7	7/19
RNP	Thambarawa	B	12	12/24
RNP	Katagamuwa	E	4	4/7
UWNP	UWNP I	D	3	3/?
UWNP	UWNP II	E	4	4/?
Mirrijjawila	Mirrijjawila	F	3	3/?

ca) with group-living females and solitary males, while considered unique within the order Carnivora (Gompper et al. 1997), parallels the social organization of elephants. However, while coati bands primarily consisted of highly related individuals, some also contained unrelated individuals (Gompper et al. 1997). The social organizations of African elephants and sperm whales (*Physeter macrocephalus*) are considered to be behaviorally convergent (Connor et al. 1998; Weilgart et al. 1996). Although genetic analysis of sperm whales has revealed that particular mitochondrial haplotypes were characteristic of female groups, all sampled groups contained more than one haplotype (Richard et al. 1996), hence unrelated females. Therefore the matriarchal social system of Asian elephants, if found to consist entirely of perfect matrilines of associating females, would be unusual among mammals.

Of the three levels of social organization described for female elephants (family group, kinship group, and clan), that represented by the female groups of Asian elephants we observed is most compatible with the "family group". The low level of association between group members [29% (observational data) and 18% (telemetry data) vs 70–90% reported for African savanna elephants (Lee 1991)] and the solitary ranging of females without dependent offspring observed by us in Asian elephants, indicate a lesser degree of association between family members than in African savanna elephants.

Although all four groups from RNP had proximal or overlapping ranges, we failed to observe any association between members of different family groups, including those that shared the same mitochondrial haplotype and greatly overlapping home ranges. Our genetic analysis found co-existing groups in both RNP and UWNP to have different haplotypes, demonstrating a lack of maternal relatedness. While the number of groups sampled was too low to be conclusive, our genetic and behavioral data do not support social groupings of greater complexity than the family group (as described for African savanna elephants) in Asian elephants. Therefore, rather than a model of population expansion over time causing group fission with continued association of daughter groups leading to a highly complex hierarchical social structure, our findings suggest a simpler model in which fission of family groups leads to daughter groups, which become largely independent of each other.

The greater overlap in the home ranges of the two groups sharing a single haplotype (Yala I and II) may indicate a greater degree of tolerance in sharing resources between "related" groups, and hence a higher order social structure. However, since we did not observe any association between members of the two groups, the definition of such a "social structure" would necessarily be different to that of African savanna elephants.

Many of the advantages of group living, such as increase in feeding efficiency, exploitation of a highly unstable environment, and amelioration or modification of the environment (Kaufmann 1974) do not apply to elephants. The main benefit of group living for elephants has been suggested to be greater success in rearing offspring (Lee 1991), which is likely to be realized through interaction with close relatives. Thus, a simpler social organization limited to the family level would also be in accord with expectations of kin selection theory (Smith 1964) and the concept of inclusive fitness (Hamilton 1964), as in elephants, altruistic behavior would be favored by selection only among close female relatives. For Asian elephants, benefits of associating with more distant relatives at the levels of kinship groups or clans are difficult to perceive and, if any, as a forest-living

mega-herbivore, are more likely to be offset by the greater costs of associating in large groups.

Larger group sizes in species inhabiting open habitat such as savanna, and smaller group sizes in species inhabiting forest habitat, are typical of mammals, and may be related to patterns of resource distribution (Clutton-Brock and Harvey 1977; Geist 1974; Jarman 1974; Kaufmann 1974; Wilson 1975). The difference in the social structure described for African savanna elephants and that we observed for forest-living Asian elephants, appears to conform to this general pattern. Costs of group living, such as competition for resources, could be a major determinant of group size for forest-living Asian elephants, and may explain the less complex social structure we observed. Comparison of the social structure of African forest elephants (*L. africana cyclotis*), which are reported to have small female groups (Fay and Nichols 1999), with that of Asian elephants and African savanna elephants, may further corroborate the importance of ecological determinants in the evolution of elephant social structure.

Although protection from predators is one of the main advantages of group living for many species (Krebs and Davies 1984; Wilson 1975), the sheer size of elephants excludes any predator threat to adults. While young may reportedly be taken by large predators on occasion (Barnett 1991), whether this occurs to an extent sufficient to influence the evolution of behavior is unknown. As the top predator in Sri Lanka is the leopard (*Panthera pardus*), which poses no threat even to elephant calves, the absence of a threat from predators in Sri Lanka also has to be considered an explanation for the smaller and looser social groupings observed by us. Study of social organization of Asian elephants on the mainland where a predatory threat exists from the tiger (*Panthera tigris*) would provide a useful comparison in this regard.

Our study suggests that the social organization of Asian elephants differs significantly from that of African savanna elephants. This finding warrants investigation of other populations of Asian elephants to determine if the social structure we observed is characteristic of the species. Application of our methods for molecular genetic sampling to Asian elephants on the mainland, and to African savanna and forest elephants, together with high-resolution studies using nuclear microsatellite markers, may further our understanding of elephant social organization and its evolution.

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References

Amos B, Schlotterer C, Tautz D (1993) Social structure of pilot whales revealed by analytical DNA profiling. Science 260: 670–672

Arnason U, Xu X, Gullberg A (1996) Comparison between the complete mitochondrial sequence of *Homo* and the common chimpanzee based on nonchimeric sequences. J Mol Evol 42: 145–152

Avise JC (1994) Molecular markers: natural history and evolution. Chapman & Hall, New York

Barnett J (1991) Disease and mortality. In: Eltringham SK (ed) The illustrated encyclopedia of elephants. Salamander, London, pp 48–63

Baskaran N, Balasubramanian M, Swaminathan S, Desai AJ (1993) Home range of elephants in the Nilgiri Biosphere Reserve, South India. In: Daniel JC, Datye H (eds) A week with elephants. Proceedings of the International Seminar on Asian elephants. Bombay Natural History Society, Bombay, pp 298–313

Brockelman WY, Reichard U, Treesucon U, Raemakers JJ (1998) Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). Behav Ecol Sociobiol 42:329–339

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. J Zool Lond 183:1–39

Connor RC, Mann J, Tyack PL, Whitehead H (1998) Social evolution in toothed whales. Trends Ecol Evol 13:228–232

Desai A (1995) Development of wildlife conservation and protected area management – Consultancy on elephant management and research including radio telemetry: Final report. Department of Wildlife Conservation, Colombo, Sri Lanka

Douglas-Hamilton I (1973) On the ecology and behavior of the Lake Manyara elephants. E Afr Wildl J 11:401–403

Douzery E, Randi E (1997) The mitochondrial control region of Cervidae: evolutionary patterns and phylogenetic content. Mol Biol Evol 14:1154–1166

Eltringham SK (1982) Elephants. Blanford Press, Poole, Dorset, UK

Fay M, Nichols M (1999) Forest elephants. Natl Geogr 195:100–113

Fernando P, Pfrender ME, Encalada SE, Lande R (2000) Mitochondrial DNA variation, phylogeography and population structure of the Asian elephant. Heredity 84:362–372

Geist V (1974) On the relationship of social evolution and ecology in ungulates. Am Zool 14:205–220

Gerloff U, Schlotterer C, Rassmann K, Rambold I, Hohmann G, Fruth B, Tautz D (1995) Amplification of hypervariable simple sequence repeats (microsatellites) from excremental DNA of wild living bonobos (*Pan paniscus*). Mol Ecol 4:515–518

Girman DJ, Mills MGL, Geffen E, Wayne RK (1997) A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus).* Behav Ecol Sociobiol 40:187–198

Gompper ME, Gittleman JL, Wayne RK (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim Behav 53:781–797

Hamilton WD (1964) The genetical evolution of social behavior. J Theor Biol 7:1–52

Hashimoto C, Furuichi T, Takenaka O (1996) Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): sequencing the D-loop region of mitochondrial DNA. Primates 37:305–318

Hoss M, Kohn M, Paabo S, Knauer F, Schroder W (1992) Excrement analysis by PCR. Nature 359:199

Irwin DM, Kocher TD, Wilson AC (1991) Evolution of cytochrome b gene of mammals. J Mol Evol 32:128–144

Jarman PJ (1974) The social organization of antelope in relation to their ecology. Behaviour 48:215–267

Kaufmann JH (1974) The ecology and evolution of social organization in the kangaroo family (Macropodidae). Am Zool 14: 51–62

Kohn M, Wayne RK (1997) Facts from feces revisited. Trends Ecol Evol 12:223–227

Kohn M, Knauer F, Stoffella A, Schroder W, Paabo S (1995) Conservation genetics of the European brown bear – a study using excremental PCR of nuclear and mitochondrial sequences. Mol Ecol 4:95–103

Krebs JR, Davies NB (1984) Behavioral ecology: an evolutionary approach, 2nd edn. Sinauer, Sunderland, Mass

Lee P (1991) Social life. In: Eltringham SK (ed) The illustrated encyclopedia of elephants. Salamander, London, pp 48–63

Leuthold W (1977) Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. Z Saeugetierkd 42:358–379

McKay GM (1973) Behavior and ecology of the Asiatic elephant in Southeastern Ceylon. Smithson Contrib Zool 125

Mohr CO (1947) Table of equivalent populations of North American mammals. Am Midl Nat 37:223–249

Morin PA, Moore JJ, Chakraborty R, Jin L, Godall J, Woodruff DS (1994) Kin selection, social structure, gene flow, and the evolution of chimpanzees. Science 265:1193–1201

Moss CJ, Poole JH (1983) Relationships and social structure of African elephants. In: Hinde RA (ed) Primate social relationships. Blackwell, Boston, pp 315–325

Packer C, Gilbert DA, Pusey AE, O'Brien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562–565

Pamilo P, Gertsch P, Thoren P, Perttu S (1997) Molecular population genetics of social insects. Annu Rev Ecol Syst 28: 1–25

Pusey AE, Packer C (1987) The evolution of sex-biased dispersal in lions. Behaviour 101:275–310

Richard KR, Dillon MC, Whitehead H, Wright JM (1996) Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proc Natl Acad Sci USA 93:8792–8795

Smith JM (1964) Group selection and kin selection. Nature 201: 1145–1147

Sukumar R (1989) The Asian elephant: ecology and management. Cambridge University Press, Cambridge

Sukumar R (1994) Elephant days and nights. Oxford University Press, Oxford

Weilgart L, Whitehead H, Payne K (1996) A colossal convergence. Am Sci 84:278–287

White GC, Garrot RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego

Wilson EO (1975) Sociobiology: the new synthesis. Belknap Press of Harvard University Press, Cambridge, Mass