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Matriarchal associations and reproduction in a remnant subpopulation of desert-dwelling elephants in Namibia

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Abstract

This study focused on a subpopulation of desert-dwelling elephants in the Kunene region of north-western Namibia, where rainfall and resources are scarce, and the rate of reproduction and recruitment is low. This subpopulation can be considered a remnant; its oldest members are survivors of the war-related poaching that occurred in the region during the 1970s and 1980s, and its numbers have still not recovered to pre-war levels. Unlike less disturbed elephant populations with strong, multi-tiered matrilineal associations, previous research suggested that the associations in the Kunene subpopulation involved only loose affiliations lacking strong social bonds. Taking that study a step further, this manuscript examines the social structure of all adult females (n=14) in the subpopulation, based on observational data combined with mitochondrial DNA (mtDNA) sequence data. A network analysis was generated from nearly eight years of association data. It was found that female desert-dwelling elephants live in first-tier/family units or small second-tier/family groups, and in at least two cases these include unrelated adult females. Associations at the level of third-tier/bond groups are rare and transitory, and there was no evidence of these being dominated by a single female or matriarch. The matrilineal social structure in this subpopulation is consistent with reports from other poached or culled elephant populations in Africa. Collectively, the results of these studies are inconsistent with the classic model of elephant social structure—stable, strictly matrilineal societies—especially in cases where poaching or culling has occurred, even if it transpired decades previously.

Key words: matriarchal associations, desert-dwelling elephants, Namibia

Résumé

Cette étude a porté sur une sous-population d'éléphants du désert dans la région de Kunene au nord-ouest de la Namibie, où la pluviométrie et les ressources sont rares, et où le taux de reproduction et de recrutement est faible. On peut considérer cette sous-population comme un vestige; ses membres les plus âgés sont des survivants du braconnage lié à la guerre qui s'est produite dans la région durant les années 1970 et 1980 et ses effectifs n'ont toujours pas atteint les niveaux d'avant-guerre. Contrairement aux populations d'éléphants moins perturbés ayant des associations matrilinéaires fortes à plusieurs niveaux, des recherches antérieures ont suggéré que les associations de la sous-population de Kunene ne comprennent que des affiliations faibles n'ayant pas de liens sociaux forts. En poursuivant cette étude plus loin, ce manuscrit examine la structure sociale de toutes les femelles adultes (n=14) de la sous-population, en se basant sur les données d'observation combinées avec les données de séquences d'ADN mitochondrial. Une analyse du réseau a été générée à partir des données d'association couvrant près de huit ans. On a constaté que les éléphants femelles du désert vivaient dans des unités familiales à un seul niveau ou dans de petits groupes familiaux à deux niveaux, et dans au moins deux cas, ces unités comprenaient des femelles adultes non apparentées. Des associations ayant des groupes avec des liens au troisième niveau sont rares et transitoires, et il n'y avait aucune preuve que celles-ci étaient dominées par une seule femelle ou une matriarche. La structure sociale matrilinéaire de cette sous-population est semblable aux rapports d'autres populations d'éléphants braconnés ou abattus sélectivement en Afrique. Collectivement, les résultats de ces études ne ressemblent pas au modèle classique de la structure sociale de l'éléphant - de sociétés stables, strictement matrilinéaires - surtout dans des cas où le braconnage ou l'abattage sélectif ont eu lieu, même si cela s'était produit des décennies auparavant.

Introduction

Social structure in African elephants

Sociality in African elephants is organized around groups of related females and their dependent offspring, usually led by the eldest female (matriarch) (Buss, 1961; Buss & Smith, 1966; Moss, 1982).

Moss and Poole (1983) and Poole (1996) defined a 'family unit' as the basic unit of elephant society, which consists of an individual female and her dependent offspring. 'Family groups' are related adult females with dependent offspring, who associate. Family groups form defensive units and kin-based allegiances, which in turn may have a positive effect on calf survival rate (McComb et al., 2001; Archie et al., 2006). 'Bond groups' or 'kinship groups' are made up of several closely related family groups. Bond groups form when family groups become too large and split along family lines. When bond groups meet, elaborate greeting behaviours are often exhibited (Douglas-Hamilton, 1972, 1975; Moss, 1982). Families and bond groups that have the same seasonal ranges are classified as 'clans'. Clans are used to define a level of association around habitat use and it is unclear whether it is a functioning elephant social unit (Poole, 1996).

Wittemyer et al. (2005, 2009) recently refined the description and quantitative basis of this fission–fusion social organization in terms of a four-tiered system: a breeding female and her sexually immature offspring are the base social unit, termed first-tier unit. Multiple first-tier (mother–calf) units in association are termed second-tier groups, also referred to as family or core groups.

Second-tier groups coalesce to form third-tier social groups corresponding to bond or kinship groups. These in turn are nested within fourth-tier groups corresponding to clans.

Early studies of elephant populations such as those in Amboseli found that female associations were strictly matrilineal, and that second-tier/family groups were comprised of related adult females (Moss & Poole, 1983). More recent studies of elephant populations, including those in Amboseli, have combined data on home range size, association indices and genetic relatedness in order to provide new insights into elephant population structure and sociality (Nyakaana & Arctander, 1999; Nyakaana et al., 2001; Charif et al., 2004; Archie et al., 2006a,b; Okello et al., 2008; Pinter-Wollman et al., 2008, 2009; Gobush et al., 2009; and Wittemyer et al., 2007, 2009).

Several of these studies found that, in populations that had undergone severe social disruption (from poaching or culling), second-tier/family groups were often comprised of females who were unrelated (i.e. did not share mtDNA). These groups were presumably the result of fusion of unrelated first-tier/family units, or the adoption of orphaned individuals or sole survivors. Results of extensive genetic analyses (mtDNA and microsatellites) in Amboseli (Archie et al., 2006a) and in the Samburu and Buffalo Springs National Reserves (Wittemyer et al., 2001, 2009), made it clear that elephant associations are not strictly matrilineal, but follow a gradient from high genetic relatedness at first and second tiers, to not significantly different from random at fourth tiers. Poaching and/or large-scale social disruption due to severe drought could have led to this shift in relationship, with more unrelated individuals being found in second-tier/family groups, such as in the more heavily poached Samburu and Buffalo Springs National Reserves.

The strongest genetic effects of poaching in an East African elephant population were reported by Gobush et al. (2009) from Mikumi National Park, Tanzania. The Mikumi population experienced heavy poaching—a 75% reduction in the population—prior to CITES's listing of African elephants as an Appendix I species in 1989. Although some poaching still occurs, it has dramatically diminished in intensity as a result of the ivory ban. Gobush et al. (2009) reported that the majority of groups (n=77) were found to contain only 2 to 3 adult females, and 45% of these were classified as genetically disrupted (e.g. either matrilineally unrelated with different mtDNA haplotypes or having the same mtDNA haplotype but unrelated at nuclear loci). In addition, the relatedness of individuals was substantially lower for a given level of association as compared to populations that did not experience poaching. Similar results were reported from another heavily poached population in northern Zambia; Owens and Owens (2009**)** found that age structure and sex ratio were skewed, the mean second-tier/family group size was reduced and that 37% of second-tier/family groups contained no females older than 15 years. Collectively, the results of these studies shake up the classic model of elephant social structure—stable, strictly matrilineal societies—especially in cases where poaching or culling have occurred, even if that poaching or culling occurred decades previously.

Desert-dwelling elephants of the Kunene region, Namibia

The history of elephants in the Kunene region is largely unknown due to the remoteness and ruggedness of the area. The first government overland vehicle to the western Kunene (Hoarusib and Hoanib Rivers) was a rescue expedition to the Skeleton Coast in 1945 (Marsh, 2008). One of the first systematic surveys of elephants in the region was made by G.L. Owen-Smith (an agricultural official for the Kaokoveld Territory, 1968-1970) who estimated there were 70 elephants occupying the Hoarusib River in 1968-1970, from the upper Hoarusib Gorge to the coast (Owen-Smith, 1970, and pers. comm.) Subsequently, aerial surveys during the wars, the period from 1975–1989 (Desert Research Foundation, undated) suggested large-scale displacement of elephants in the western Kunene, including the loss and subsequent re-colonization of elephants in the lower Hoarusib River. Additionally, a subpopulation in the western end of the Kunene River, which was known to make annual migrations south to the Hoarusib River, was also lost to poaching by 1980 (Viljoen, 1988).

Three previous studies have reported on the social structure of desert-dwelling elephants in Namibia (Viljoen, 1988**;** Lindeque & Lindeque, 1991; Leggett et al., 2003.) Viljoen's study (1988) was conducted during the period 1980–1983 in the western Kunene, a period of severe drought and heavy poaching at the time of the Namibian War of Independence (1966–1989) and the Angolan War (1975–2002). Part of his study focused on a subpopulation of desert-dwelling elephants in the north-western Kunene region. In this subpopulation Viljoen observed a social structure similar to that reported by Douglas-Hamilton (1972), Martin (1978) and Moss and Poole (1983), except that the age structures of several family groups suggested the loss of older adult females (matriarchs) due to poaching. Viljoen had to presume the relatedness of individuals within family groups because genetic tools were not available at that time, and the limited duration of the study did not allow for deciphering relatedness in such a long-lived species. He found an increase in average group size during the wet season as a result of feeding aggregations.

Lindeque and Lindeque (1991) suggested that this subpopulation reflected a remnant core elephant society, presumably as a result of the wars and concomitant poaching. Their study, however, focused on the range and movement of a limited number of radio-collared elephants and did not examine elephant socio-ecology.

Based on preliminary observational data, Leggett et al. (2003) suggested that the associations between first-tier/family units in this subpopulation involved only loose affiliations lacking strong social bonds**.** Taking the preliminary observations of Leggett et al. (2003) a step further, this paper examines the social structure of all adult female elephants in this subpopulation, based on eight years of observational data combined with mitochondrial DNA sequence data.

Methods

Study area

The study area is located in the Kunene province of north-western Namibia (Fig. 1) in an extremely arid

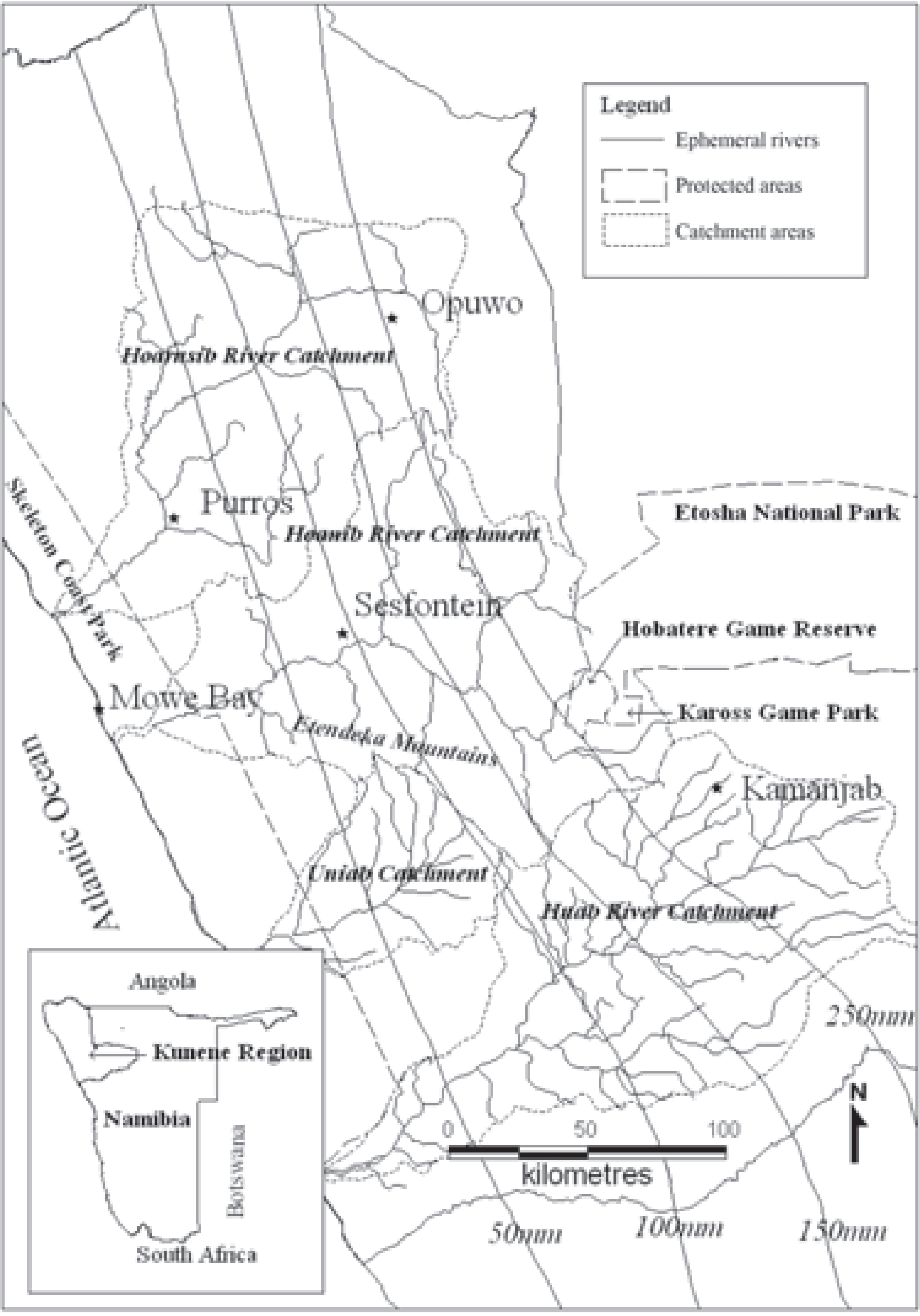

Figure 1. Map of the study area in Namibia showing the four primary river catchments used by desert-dwelling elephants. This study focused on the permanent family groups inhabiting the Hoarusib and Hoanib catchments, west of the 100 mm isohyet.

area where rainfall is spatially and temporally variable and averages less than 100 mm annually (Viljoen, 1988). Distant rainfall in the upper reaches (over 60 km to the east) of the Hoarusib and Hoanib River catchment areas typically produce brief seasonal flooding during the wet season, February–May (after Viljoen, 1988), even if no rain falls in the immediate area. These western-flowing ephemeral rivers carry little surface water except in canyons where bedrock forces it to the surface, and for most of the year the water flows underground (Jacobson et al., 1995). In this desert environment the ribbons of vegetation along the ephemeral rivers represent 'linear oases' where elephants and other wildlife find forage and water during the dry season. Elephants occupy these ephemeral rivers most of the year in predictable home ranges (Viljoen, 1988; Leggett et al., 2003; Leggett, 2006). Female elephants move up and down these riverbeds and tributaries, sometimes to the ocean, and make periodic 70 km migrations between the two rivers. Migration often occurs in response to the abundant ripening of *Faidherbia albida* pods, a protein source that is highly sought after by elephants and other herbivores. During the wet season, elephants range beyond these river drainages, initially on foraging expeditions in search of *Commiphora* spp. bushes, and later for other forage as rainfall brings a green-up of vegetation (Viljoen, 1987, 1988, 1989a, 1989b; Viljoen & Bothma, 1990; Leggett, 2006).

Human habitation in the region is concentrated in and upstream of the town of Purros along the ephemeral Hoarusib River and in, and upstream of Sesfontein along the Hoanib River, but also includes a handful of tourist camps between the towns and the Skeleton Coast National Park (SCNP). Self-drive and guided tourists move up and down the rivers during the dry season; however, most are restricted from entering SCNP, which extends from the coast approximately 30 km inland.

Identification of individuals in the Hoarusib/Hoanib subpopulation

All elephants in the subpopulation have been individually identified using a combination of photographs and identification sheets. The photographic techniques used were similar to those already described by Altmann (1974), Douglas-Hamilton and Douglas-Hamilton (1975), Moss (1982) and Sukumar (1989), and elephants were aged by size (Laws, 1966). Each elephant is assigned a number beginning with WKF or WKM (western Kunene female or western Kunene male), and offspring of an individual female are labelled *a1, a2, a3* etc., according to birth sequence. When offspring reach sexual maturity (for females, at birth of first offspring; for males, at departure from the family unit) they are assigned an adult number. Groups are classified according to the oldest female; for example, a second-tier/family group that contains four adult females (WKF-3, WKF-11, WKF-14 and WKF-15) is referred to as WKF-14's group, as she is the oldest female in the group.

Quantification of observed associations among adult females

The observations reported here were made between 2002 and 2009 (n=397). Monthly surveys were conducted in the study area (weather and floods permitting) and observations of individual identifications, location, numbers, and behaviour were recorded. Elephants were considered to associate if they were observed within 500 m of each other (Wittemyer et al., 2005; Pinter-Wollman et al., 2008). However, the majority of the observations of association involved obvious social interactions and were made at distances much closer than 500 m. Only one observation of association was recorded for any pair of individuals each day.

Association indices (AI) for all pair-wise combinations of adult females were calculated using the methods of Ginsberg and Young (1992). The program Cytoscape 2.6.3 (Shannon et al., 2003) was used to plot pair-wise AI among adult female elephants. To cluster these into a network we used the stochastic spring-embedded algorithm, as implemented in Cytoscape (Ley et al., 2008). The strength of the social bond or AI between elephants is indicated by line thickness.

Mitochondrial DNA genotyping

Genetic material was obtained from fresh faecal samples of known individuals in the subpopulation. Approximately 5 g of the surface material of fresh faeces were collected using a new pair of sterile gloves for each collection. Samples were air dried and stored in paper bags prior to DNA extraction. After drying, a flame-sterilized razor blade was used to scrape the surface of dried faeces to obtain sloughed intestinal cells. Strict contamination control procedures were observed during the scraping and extraction process

(Ramey et al., 2000). DNA was then extracted using a QIAGEN Stool DNA kit and modifications described by Wehausen et al. (2004).

A fragment of the control region was PCR-amplified using primers LafCr1 and LafCr2, as described in Nyakaana and Arctander (1999) with the following modifications to PCR conditions: 94°C denature for 2 min., followed by 37 cycles of 95°C for 30 sec., 47°C for 30 sec., and 72°C for 45 sec. Cycle sequencing was performed on both strands at an annealing temperature of 48°C with primers LafCr1, LafCr2, and an internal primer BETH (ATGGCCCTGAAGAAAGAACC) that was designed for the first conserved sequence block of the control region (Charif et al., 2004). A second PCR was used to obtain additional control region sequence, utilizing the reverse compliment of BETH and a new primer PreRPT-r (GTCCTCCGAGCATTGACTGAA) with the following PCR conditions: 94°C denature for 2 min., followed by 37 cycles of 95°C for 30 sec., 50°C for 30 sec., and 72°C for 45 sec. Cycle sequencing was performed on both strands at an annealing temperature of 48°C. Unincorporated dye terminators were removed with DyeEx spin columns (QIAGEN), and the reactions run on an ABI373XL automated DNA sequencer. Chromatograms were compiled and edited using the program Sequencher 4.0 (GeneCodes). The combined mtDNA sequences were 829 bp in length.

Results

Population size and reproduction

As of 2009, there remain only 14 adult female elephants in the Kunene subpopulation that spans the Hoarusib and Hoanib Rivers. These 14 females assort roughly into five second-tier/family groups of 2–4 adult females and their offspring. The total number of subadults, juveniles, and calves in the subpopulation is presently 19, bringing the number of females and offspring to 33. When adult males (n=17) who frequent the area are added in, the total number of elephants in the subpopulation may exceed 50 (although fewer are typically present). There are six remaining adult males over the age of 25 who frequent the Hoanib and Hoarusib. The mean calving interval (e.g. years of observation x number of adult females/calves born) of this subpopulation was 9.1 years, although three females have produced two calves during the study (e.g. every 4–5 years). Calf survival to one year of age was 67% (8 out of 12 observed calves), although this figure cannot account for newborns that may have died before they were observed, and whose carcasses were never found.

Over the eight years of the study, the number of adult females has remained fairly constant, at around 14 (Table 2). Two adult females in the subpopulation died—WKF-10 in 2002, of natural causes and WKF-17 in 2006, of gunshot wounds (orphaning her calf). One adult female, WKF-19, joined the subpopulation, presumably from another subpopulation to the south.

Table 1. Composition of elephant groups in Hoarusib and Hoanib Rivers, showing the oldest female in each family group and associated adult females during the course of this study. The number of subadults and juveniles observed during the 2009 hot-dry season are shown in the third column.

Oldest adult female in each family group	Associated adult females	Number of subadults, juveniles, and calves
WKF-1	WKF-2	3
WKF-4	WKF-19	3
WKF-7		2
WKF-8	WKF-13	0
WKF-14	WKF-15, WKF-3, (WKF-10*), WKF-11	7
WKF-16		1
WKF-18	(WKF-17**), WKF-12	2

*Died in 2002 **Died in 2006

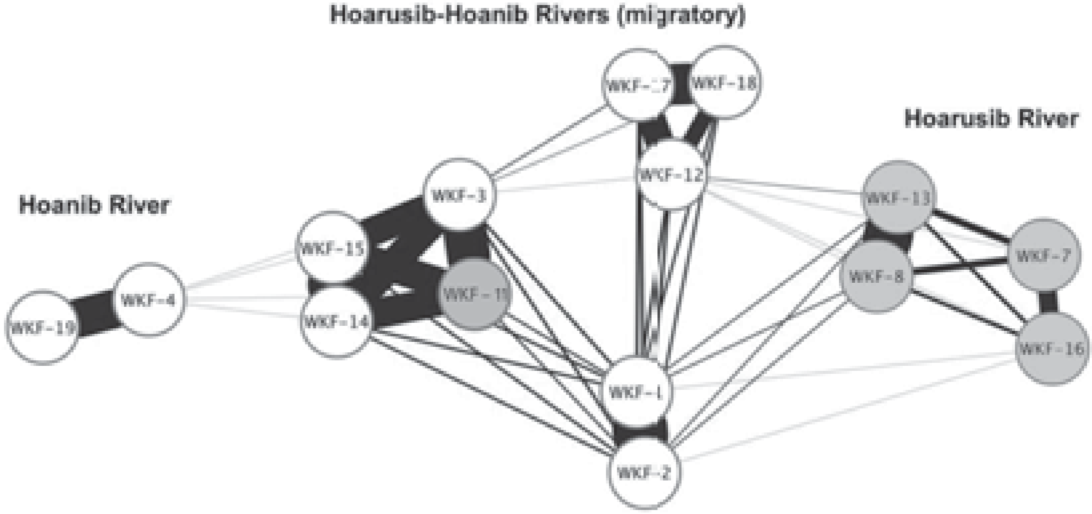

Figure 2. Social network of adult female desert-dwelling elephants near the Hoarusib and Hoanib Rivers in the western Kunene. Network nodes represent individual elephants and connecting lines denote their associations (AI). Line thickness denotes association strength: the thicker the line, the greater the AI value (frequency of two individuals observed together). If individuals were never observed together, no line is drawn between them. MtDNA haplotypes are indicated by shading: haplotype ‘A’ (open circle), haplotype ‘B’ (dark grey, WKF-11), and haplotype ‘C’ (pale grey, WKF-7, 8, 13, and 16). The home range of family groups, by river catchment, is indicated. The migration between the Hoarusib and Hoanib Rivers is a distance of approximately 70 km, through waterless terrain.

The total number of females (of all ages) was 22 in 2002, and 23 in 2009. In terms of reproduction, 12 calves were born between January 2002 and November 2009; however, one-third of these calves (n=4) died within their first year. Overall this subpopulation increased by approximately 1.5% annually.

Associations and social organization

A network analysis obtained from association data among adult female desert-dwelling elephants in the Hoarusib and Hoanib Rivers is presented in Fig. 2.

Adult females WKF-1 and WKF-2, mother and daughter, were always observed together and therefore had an AI of 1.0 (Refer to Table 3 for all pairwise association indices.). Adult females WKF-8 and WKF-13, presumed to be mother and daughter, were consistently observed together, except for a few occasions, and had an AI of 0.93. All other associations between adult females were less than 0.93, indicating that they frequently associated, but it was not unusual to find them with just their immediate first-tier/family unit or in second-tier/family groups of two females and offspring. For example, within WKF-14’s family group, WKF-3 and WKF-11 often form one subgroup (AI=0.85), while WKF-14 and WKF-15 form another (AI=0.83). These shifts from first-tier/family units to second-tier/family groups change the size of female herds observed in the study area.

Associations at the level of third-tier/bond groups are rare and transitory (Fig. 2), with little greeting or social interaction upon meeting, as compared to other elephant populations that have been extensively studied (e.g. Moss & Poole, 1983). There was no evidence that the rare third-tier/bond groups were dominated by a single female or a matriarch.

One adult female in the subpopulation who does not readily associate with other adult females is WKF-4. Her home range is restricted to the Hoanib River and its tributaries. Until the appearance of WKF-19 in 2007, WKF-4 had only been observed infrequently in the company of WKF-14’s group, and no others.

Genetic relatedness and associations

Three mtDNA haplotypes were identified from the 14 females analyzed. Polymorphic sites in the mtDNA sequenced from elephants in this study are presented in Table 2.

Adult females having mtDNA haplotype ‘B’ (WKF-8, WKF-13, WKF-16, WKF-7) only

Table 2. Variable nucleotides in the DNA sequences for each mtDNA haplotype (GenBank accession numbers JN129997- JN129999)

mtDNA haplotype	Variable base positions in mtDNA sequence			Adult female
	311	349	389	
'A'	T	A	A	WKF-1, 2, 3, 4, 12, 14, 15, 17, and 18
'B'	T	G	A	WKF-7, 8, 13, and 16
'C'	C	A	G	WKF-11

NB: WKF-19, a female who emigrated into this subpopulation in 2007, was not sampled.

infrequently associate with two other groups, WKF-1's and WKF-18's groups (haplotype 'A'), and no others. Interactions within the 'B' haplotype family group showed close associations between WKF-8 and WKF-13, and WKF-7 and WKF-16, respectively. These latter two spend the majority of their time with their own calves (as first-tier/family units) rather than in a second-tier/family group with WKF-8 and WKF-13.

The females that make up WKF-14's second-tier/family group include WKF-15 (her daughter), WKF-3, and WKF-11. The first three females have the same mtDNA haplotype ('A'), but WKF-11 is unique, the only female in the subpopulation with mtDNA haplotype 'C'. Association indices reveal that she is most closely associated with WKF-3 (AI=0.780), and secondly with WKF-14 and WKF-15 (AI= 0.980). Although not closely related to the others in her second-tier/family group, she nonetheless associates with them consistently, albeit usually more at the periphery. It is not known when or how she came to be associated with this second-tier/family group, but hers is an obvious example of association that is not strictly matrilineal.

Within WKF-18's second-tier/family group is WKF-12. While she shares the same mtDNA haplotype ('A'), she does not share any microsatellite alleles at six loci that were surveyed (unpublished data). According to R. Loutit (pers. comm.), WKF-12 was captured in the 1980's in the Huab River, and her ears were marked. She subsequently migrated to the Hoanib and Hoarusib Rivers, where she is sometimes observed in association with WKF-18.

Discussion

This study focused on a subpopulation of desert-dwelling elephants in north-western Namibia, where rainfall and resources are scarce, and the long calving interval and rate of population increase is at the low end of reported values for African elephants. In African savannah- and dry bush-dwelling elephants, second-tier/family group size averages between 8 and 12 individuals (Moss & Poole, 1983). In contrast, desert-dwelling elephants in the Kunene have smaller second-tier/family group sizes of typically four to eight individuals (Viljoen, 1988; Leggett, 2003). Poole (1994) reported from Kenya that finding a lone female elephant or even a lone set of two to three females over an extended period of time would be an unusual occurrence in the wild. In the western Kunene region of Namibia however, this is the norm. Female desert-dwelling elephants live in first-tier/family units or small second-tier/family groups, and in at least two cases these include unrelated adult females. This pattern is consistent with that reported from other poached or culled populations (Nyakaana et al., 2001; Charif et al., 2005; Gobush et al., 2009).

It is unknown to what extent the close associations of unrelated adult females may date back to the heavy poaching of elephants that occurred during the Namibian War of Independence (1966–1990) and the height of the Angolan War (1970s and 1980s); however, the poaching was severe. Viljoen (1988) summarized the history of the desert-dwelling elephants as follows:

> …elephants in the Kaokoveld (now known as the Kunene) show a marked attachment to their various home ranges in spite of having unlimited movement in nearly all directions. They could be driven out of their home ranges or temporarily moved out over long distances but the elephants always returned to their original home ranges. This behaviour has caused the extermination of entire herds.

Table 3. Association indices of adult female elephants in the study area, based on observations from January 2002 through January 2009

	WKF-1	WKF-2	WKF-3	WKF-4	WKF-7	WKF-8	WKF-11	WKF-12	WKF-13	WKF-14	WKF-15	WKF-16	WKF-17	WKF-18	WKF-19
WKF-1	1.000														
WKF-2	1.000	1.000													
WKF-3	0.054	0.054	1.000												
WKF-4	0.000	0.000	0.010	1.000											
WKF-7	0.000	0.000	0.000	0.000	1.000										
WKF-8	0.030	0.030	0.000	0.000	0.130	1.000									
WKF-11	0.040	0.040	0.780	0.010	0.000	0.000	1.000								
WKF-12	0.060	0.060	0.010	0.000	0.010	0.010	0.000	1.000							
WKF-13	0.030	0.030	0.000	0.000	0.130	0.880	0.000	0.020	1.000						
WKF-14	0.050	0.050	0.530	0.010	0.000	0.000	0.540	0.000	0.000	1.000					
WKF-15	0.050	0.050	0.530	0.010	0.000	0.000	0.540	0.000	0.000	0.980	1.000				
WKF-16	0.010	0.010	0.000	0.000	0.340	0.070	0.000	0.010	0.070	0.000	0.000	1.000			
WKF-17	0.060	0.060	0.030	0.000	0.000	0.000	0.000	0.520	0.000	0.000	0.000	0.000	1.000		
WKF-18	0.050	0.050	0.020	0.000	0.000	0.000	0.000	0.300	0.000	0.000	0.000	0.000	0.740	1.000	
WKF-19	0.000	0.000	0.000	0.700	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000

> Examples of this are the northern elephant population, which numbered 160 in 1970 (Owen-Smith, 1970), only to be shot out except for eight cows by 1977. These cows were almost continuously hunted until they too were killed in 1980 in the same area. Another example is the elephant herds of the middle Hoarusib River where Woods counted 100 elephants in 1951 (in: Green, 1952) but by 1977 this group had dwindled to 14 (Viljoen, 1988). In 1980 there were only four cows left who were continuously harassed and shot at by the resident people. Although these cows temporarily joined other herds for short periods they repeatedly returned to the original home range until they too were killed in April 1981. Similarly, elephants that frequented the Hartman Valley - Kunene River region numbered 40 in 1970 (Owen-Smith, 1970), eight in 1977 (Viljoen, 1988) and at present consist of only six cows and no bulls. Although these cows had on two occasions joined elephants in the western Hoarusib River, they returned over a distance of 195 km to their original home range along the Kunene River [and were subsequently shot and killed].

Viljoen (1988) also reported that, by 1980, the western subpopulation (Hoarusib, Hoanib and Uniab Rivers) consisted of 86 individuals, and by 1983 there were only 70 individuals left. The maximum number found in this region in 2009 was approximately 74 (50 in the Hoarusib and Hoanib Rivers, and potentially another 15–24 in the Uniab River and its tributaries (unpublished data from P. Stander, pers. comm.; J. Nott and R. Ramey, pers. comm.).

Because of heavy poaching in the past, and a low reproductive rate (i.e. long calving interval) due to the desert environment, it would appear that the traditional herd structure described by Douglas-Hamilton (1972) and Moss and Poole (1983) does not currently apply to desert-dwelling elephants of northwest Namibia. This combination of factors constrains the possible size of first-tier/family units and second-tier/family groups, and therefore the potential emergence of a third-tier/bond group or fourth-tier/clan hierarchy. The majority (~12) of adult females in the subpopulation are old enough (30–50 years) to have witnessed (and possibly been orphaned by) the poaching that severely depleted the western Kunene during the late 1970s and 1980s (Viljoen, 1987). Poaching may have disrupted otherwise stable matriarchal groups and the surviving females re-formed loose associations.

Compared to savannah-dwelling elephants, desert-dwelling elephants living in this marginal environment have a lower rate of reproduction, reduced rate of defecation, longer movements and much larger home ranges (Leggett et al., 2003; Leggett, 2006; Leggett, 2008). While males come and go from this subpopulation, females are very philopatric and make only infrequent movements greater than 20 km outside these rivers. The only substantial influx of female elephants into the study area was temporary: an unknown group of females and young (n=9) that was not known from the Hoarusib or Hoanib Rivers briefly occupied the remote Hoanib floodplain for several months in 2008 (pers. obs.). This group, however, has not been seen since (P. Stander, pers. comm.).

If this subpopulation experiences no female immigration, emigration, or unexpected mortality, then the number of reproductive females (e.g. the population structure) may be expected to remain approximately the same: seven subadult females (13 years or older) will be of reproductive age by 2014, an equal or greater number of adult females will be older than 40 years, and three will be more than 50 years. In eight years, the Hoarusib/Hoanib subpopulation has had a net loss of one adult female (and a net gain of only one female, all ages included). With only 14 adult females present and a net population reduction since the 1980s (Viljoen, 1988), it is apparent that the loss of any adult females could have negative consequences for this small subpopulation.

From a conservation perspective, at the current size and rate of increase (1.5% annually), it is doubtful that this desert subpopulation will soon recover to what it was in the 1960s, prior to extensive poaching. The combination of past poaching and a severe desert environment underscore the need to reduce female mortality, whether it is from human-elephant conflict, poaching or disease.

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