 doi: 10.1111/j.1365-294X.2008.03797.x

Fine-scale population genetic structure in a fission–fusion society

ELIZABETH A. ARCHIE,* JÉSUS E. MALDONADO,* JULIE A. HOLLISTER-SMITH,† JOYCE H. POOLE,‡ CYNTHIA J. MOSS,‡ ROBERT C. FLEISCHER* and SUSAN C. ALBERTS§
*Center for Conservation and Evolutionary Genetics, NZP/NMNH, Smithsonian Institution, Washington, DC 20008, USA, †Oregon Health & Science University, Portland, OR 97239-3098, USA, ‡Amboseli Trust for Elephants, Langata 00509, Nairobi, Kenya, §Department of Biology, Duke University, Durham, NC 27708, USA

Abstract

Nonrandom patterns of mating and dispersal create fine-scale genetic structure in natural populations — especially of social mammals — with important evolutionary and conservation genetic consequences. Such structure is well-characterized for typical mammalian societies; that is, societies where social group composition is stable, dispersal is male-biased, and males form permanent breeding associations in just one or a few social groups over the course of their lives. However, genetic structure is not well understood for social mammals that differ from this pattern, including elephants. In elephant societies, social groups fission and fuse, and males never form permanent breeding associations with female groups. Here, we combine 33 years of behavioural observations with genetic information for 545 African elephants (*Loxodonta africana*), to investigate how mating and dispersal behaviours structure genetic variation between social groups and across age classes. We found that, like most social mammals, female matrilocality in elephants creates co-ancestry within core social groups and significant genetic differentiation between groups (Φ_{ST} = 0.058). However, unlike typical social mammals, male elephants do not bias reproduction towards a limited subset of social groups, and instead breed randomly across the population. As a result, reproductively dominant males mediate gene flow between core groups, which creates cohorts of similar-aged paternal relatives across the population. Because poaching tends to eliminate the oldest elephants from populations, illegal hunting and poaching are likely to erode fine-scale genetic structure. We discuss our results and their evolutionary and conservation genetic implications in the context of other social mammals.

Keywords: African elephant, dispersal, kinship, mating behaviour, microsatellites, population genetic structure

Received 23 September 2007; revision accepted 4 December 2007

Introduction

Population genetic models of the distribution and loss of genetic variation in populations classically assume that patterns of mating and dispersal within populations are random and panmictic (Wright 1965). However, this assumption is usually false for social species; instead, sex-biased dispersal and limited reproductive opportunities create fine-scaled genetic structure within populations (Baker & Marler 1980; Chesser 1991a, b; Sugg *et al.* 1996; Storz 1999). This fine-scale population genetic structure has important potential consequences for both evolutionary processes and conservation genetics: it can structure opportunities for kin selection (e.g. Höglund & Shorey 2003; Hazlitt *et al.* 2004; Cutrera *et al.* 2005; Archie *et al.* 2006b; Woxvold *et al.* 2006), influence the rate of inbreeding or outbreeding (Chesser 1991a, b; Sugg 1996), impact processes of local adaptation (Storz 1999; Storz 2005), confound quantitative trait locus (QTL) studies (Ewens & Spielman 1995), and influence the rate at which genetic diversity is lost from natural populations (Melnick 1987; Chesser *et al.* 1993; Sugg 1994; Sugg 1996; Dobson *et al.* 2004).

Correspondence: E. A. Archie, Smithsonian Genetics Program, 3001 Connecticut Ave. NW, Washington, DC 20008, USA. Fax: (202) 673–4648; E-mail: archiee@si.edu

In mammals, fine-scale genetic structure is best understood for one of the most common societies; that is, societies where social group composition is stable, dispersal is male biased, males form relatively permanent associations with female social groups, and mating is polygynous such that matrilocal females all mate with the same relatively few males. Such nonrandom patterns of mating and dispersal create 'breeding group' populations where: (i) group members have high co-ancestry, (ii) social groups are genetically differentiated from each other (F_{ST} among groups is significantly greater than zero), and (iii) offspring are unusually heterozygous, given the co-ancestry within groups (F_{IS} is significantly less than zero; reviewed in Dobson *et al.* 1998; van Staaden 1995; Sugg 1996; Storz 1999). Such breeding group species include many nonhuman primates (de Jong *et al.* 1994; Turner 1981; Dracopoli *et al.* 1983; Melnick *et al.* 1984; Melnick & Pearl 1986; Melnick 1987; Pope 1992; de Ruiter & Geffen 1998; Pope 1998), social rodents (Chesser 1983; Schwartz & Armitage 1980; van Staaden *et al.* 1996; Dobson *et al.* 1997; Dobson *et al.* 1998; Dobson *et al.* 2004), some social carnivores (Spong *et al.* 2002), some bats (Wilkinson 1985), rabbits (Surridge *et al.* 1999) and rock-wallabies (Hazlitt *et al.* 2004; Hazlitt *et al.* 2006).

Less well understood is the fine-scale population genetic structure of mammals that are highly social, but whose societies differ from the breeding group paradigm. There are several such species, and among them are some cetaceans, such as sperm whales, and Asian and African elephants (Douglas-Hamilton 1972; Moss & Poole 1983; Christal & Whitehead 2001; Whitehead 2003). Their genetic structure is important, not only for illuminating underappreciated parameters that influence fine-scale genetic structure, but also because many highly social mammals, including elephants and sperm whales, are charismatic flagship species that are threatened by hunting and habitat destruction.

Elephants and sperm whales share some features in common with breeding group species — for example, males are the dispersing sex, while matrilocal females form predictable social groupings and close and enduring social partnerships (Moss & Poole 1983; Lee 1987; Moss 1988; Whitehead *et al.* 1991; Whitehead 1996; Christal, Whitehead 2001; Whitehead 2003). However, elephants and sperm whales differ from breeding group species in two important ways. First, they live in fission–fusion societies where social groups are not temporally stable, and instead divide and re-form over the course of hours, days, or weeks (Douglas-Hamilton 1972; Moss & Poole 1983; Whitehead *et al.* 1991; Whitehead 2003; Wittemyer *et al.* 2005). Second, and most relevant to population genetic structure, male elephants do not form permanent associations with female social groups. Instead, males move widely within populations, visiting many social groups as they search for sexually receptive females, and siring offspring in multiple core groups (Moss & Poole 1983; Poole 1989b; Poole & Moss 1989; Hollister-Smith *et al.* 2007); sperm whales appear to have similar behaviour patterns (Whitehead *et al.* 1991; Whitehead 1996; Christal, Whitehead 2001; Whitehead 2003). As a result, these species do not form 'breeding groups' in the strictest sense.

As yet, no data have been available to investigate the impact of these behavioural processes on population genetic structure in nonbreeding group mammalian societies. In this study, we investigate the extent to which such behaviours structure genetic variation in a natural population of wild African elephants. Several alternative outcomes are possible. In elephants, males' freedom to breed in many social groups, across the population, may reduce co-ancestry within social groups and genetic differentiation between those groups, relative to breeding group species. As a result, genetic structure in elephants may conform more closely to the predictions of panmixia than breeding group species, or it may resemble the relatively weak genetic structure of herd-living ungulates (Petit *et al.* 1997; Coltman *et al.* 2003; Nussey *et al.* 2005).

However, several aspects of elephant social behaviour may reduce panmixia and increase genetic structuring. First, females form predictable, long–term associations with female kin, even though female social groups are not territorial and have broadly overlapping home ranges (Douglas-Hamilton 1972; Moss & Poole 1983; Wittemyer *et al.* 2005). Specifically, females are matrilocal and form social units called 'core' or 'family' groups, consisting of 2–30 matrilocal adult females and their immature offspring. Kinship predicts the fission and fusion of elephant groups, and as a result, female elephants spend most of their time with their closest maternal kin (Archie *et al.* 2006b). This behaviour should result in relatively high co-ancestry within social groups and genetic differentiation between groups. Second, because male elephants reach their peak reproductive success around 40–50 years of age and maintain this peak for 5–10 years (Poole 1989b; Hollister-Smith *et al.* 2007), this reproductive peak may create cohorts of paternal relatives across the population. That is, individuals may be more closely related to individuals from their own age cohort and to their father's cohort than to the rest of the population. Third, elephants may engage in nonrandom mating even in the absence of relatively permanent male–female associations. For instance, if female elephants within a single core group all breed with the same set of males, perhaps through female choice or coordinated estrous (e.g. Moss 1983; Rossiter *et al.* 2005) this will enhance levels of co-ancestry within groups. Alternatively or additionally, male elephants may expend greater mating effort in some core groups than others, and this would also cause elephants to resemble breeding group species.

We combined 33 years of behavioural observations with genetic information for 545 elephants in a wild population. First, we tested whether nonrandom mating behaviour generated co-ancestry within core groups, and whether paternal relatives occurred in similar-aged cohorts across the population. Then, we tested whether genetic variation in the study population was panmictic or resembled that found in breeding group species. Finally, we simulated the effects of age-biased poaching on the genetic structure of core social groups by excluding the oldest females (with the largest tusks) from our data set. Our results are important, not only for understanding how genetic variation is structured in elephant populations, but also for their conservation. Most elephant populations are isolated by habitat destruction, and are thus threatened by the loss of genetic diversity.

Methods

The study population

Research subjects were the wild, free-ranging African elephants that live in and around Amboseli National Park, Kenya. These elephants have been studied continuously since 1972 by researchers working with the Amboseli Elephant Research Project (AERP) and are among the most natural and intact elephant populations in Africa (Moss 2001). The habitat in and around Amboseli is semi-arid savannah, and the elephant population currently numbers around 1400 individuals. All elephants were individually recognizable from naturally occurring physical features (e.g. tears or holes in the ears, tusk and body shape), which were recorded in a photographic database. All individuals were assigned an age. The ages of elephants born since 1975 were known to within 2 weeks, and the ages of elephants born between 1972 and 1975 were known to within 3 months. Because elephants continue to grow throughout their adult lives, the ages of elephants born before 1972 were estimated based on body size. These estimates were based on well-documented patterns of variance in shoulder height and body shape with increasing age, and were corroborated with tooth eruption data from mortalities for which skulls were recovered; age estimates of the oldest elephants were considered accurate to within 5 years (Haynes 1991; Lindeque & van Jaarsveld 1993; Lee & Moss 1995; Moss 2001; Morrison *et al.* 2005).

Elephants were categorized as calves or adults depending on their age and/or reproductive status; females were defined as adults when they had given birth at least once (first birth usually occurs between 9 and 17 years of age), and adult males were 21 years of age or older — the youngest age of genetically confirmed paternity in Amboseli (Archie *et al.* 2007). Between 1976 and 2005, Amboseli's adult females and calves lived in 54 different core social groups. Almost all of these groups persisted throughout the study; however, two groups went extinct, while another was created by permanent fission of a pre-existing group. Because female elephants are matrilocal, natal core groups were known for all females in the study. Because males disperse from their natal core groups at around 14 years of age, natal core groups were only known for males that dispersed after 1972.

Behavioural data collection

Behavioural observations began in 1972 and were opportunistic. When elephants were sighted, researchers collected several pieces of data, including individual identities, group membership, births, and deaths. Since 1976, researchers also collected observations and focal samples of female oestrus and male sexual behaviour in the presence of oestrous females. Oestrus lasts 4–5 days in female elephants, and researchers identified oestrus with diagnostic behaviours: adult male elephants expressed much greater interest in oestrous females — by smelling their genitals, urine and faeces, and attempting to copulate — and oestrous females exhibited an 'oestrous walk' during which they move away from interested males, while glancing back over their shoulder (Moss 1983; Poole 1989b). Non-oestrous females ignored male interest and did not move away from males using the 'oestrous walk'. Whenever researchers observed a female in oestrus, they recorded the identities of adult males that guarded or successfully copulated with the oestrous female. Guarding occurred when the male that was the closest mature male to the oestrous female maintained this proximity by chasing all other males that approached the oestrous female. Copulation occurred when the male mounted the female from behind, obtained intromission, and was apparently accompanied by ejaculation.

Genetic sampling and genotyping

The analyses described here used genetic samples from 545 individuals, including 256 adult females, 106 adult males, and 183 calves. Genotyping was conducted mainly from noninvasive faecal samples and a few tissue samples. Sample collection and DNA extraction methods are described extensively in Archie *et al.* (2003) and Archie *et al.* (2006b). Briefly, faeces were collected from known individuals, almost always within 10 min of defecation, and DNA was extracted using a modified protocol (Archie *et al.* 2003) for the QIAamp DNA Stool Kit (QIAGEN).

All individuals were genotyped at 11 microsatellite loci, including 10 tetranucleotide loci (LaT05, LaT07, LaT08, LaT13, LaT16, LaT17, LaT18, LaT24, LaT25, LaT26;

Archie *et al.* 2003) and one dinucelotide locus (LafMS02; Nyakaana *et al.* 1998). Polymerase chain reaction (PCR) amplification protocols are in Archie *et al.* (2003) and Archie *et al.* (2006b). PCR products were separated using either an ABI PRISM 3700 or ABI PRISM 3100 DNA Analyser, and microsatellite alleles were analysed using GENOTYPER 2.0 software (version 2.5, PE-Applied Biosystems).

To minimize genotyping errors, we conducted microsatellite genotyping according to the protocol described in Archie *et al.* (2006b). To summarize, we used a modified version of the multiple tubes approach (Taberlet *et al.* 1996). Whenever possible (89% of cases), individuals were genotyped from two faecal samples collected from independent defecations. All heterozygote genotypes were replicated at least twice and all homozygote genotypes were replicated at least seven times. A given allele was assigned to an individual only if it amplified at least twice during all replicates. Finally, Mendelian checks were conducted for all mother–offspring pairs, and all loci were in Hardy–Weinberg equilibrium.

Assigning parentage

Maternity was known from direct observation for all calves included in this study, as elephants have a long period of maternal dependence and suckle for 4 years. This enabled repeated sightings of mother–calf pairs, and hence, very accurate mother–offspring relationships. Finally, maternity was confirmed via Mendelian checks for all mother–offspring pairs.

We used CERVUS software (version 3.0; Kalinowski *et al.* 2007) to assign paternity to 152 of 183 elephant calves for whom we had complete genotypes. All calves for which paternity was assigned were born between 1978 and 2002. This represented approximately 10% of the calves born during this period. We used the following input parameters for all CERVUS simulations: 10 000 cycles, 90 candidate parents, 100% of loci typed, 1% of loci mistyped and confidence levels of 95% strict and 80% relaxed. The proportion of candidate parents sampled from the population varied over the 25-year period. Because CERVUS is sensitive to this proportion (Krutzen *et al.* 2004), we ran different simulations in CERVUS for periods with different proportions of candidate males sampled: 33% (1977–1980), 45% (1981–1985), 55% (1986–1990), 61% (1991–1995) and 74% (1996–2000) (see Archie *et al.* 2007; Hollister-Smith *et al.* 2007; for details).

A father was assigned to a calf when two conditions were met: (i) CERVUS assigned paternity with 95% confidence, and (ii) there were no Mendelian mismatches between the calf and its assigned father. Each of the 152 calves for which fathers were assigned had a unique set of parents (i.e. we found no full siblings); these parents included 42 individual males and 113 individual females.

Statistical analyses

Randomization tests of mating behaviour. In order to test whether nonrandom mating behaviour generated co-ancestry in elephant groups, we ran two Monte Carlo randomization simulations. In the first simulation, we tested whether core groups of female elephants engaged in sexual behaviour and bred with a smaller number of males than expected by chance. To do this, we used Monte Carlo randomization simulations to generate a distribution of the expected number of different males mate guarding, copulating, and siring calves per group, given the number of times we observed these males engaging in these sexual behaviours or siring offspring across the entire population. We then compared these random expectations to the observed number of different males engaging in sexual behaviour or conceiving offspring in each core group. Our hypothesis was supported if the observed number of different males was less than random expectations. Specifically, we counted the number of times any adult male was observed mate guarding or copulating between 1976 and 2004 in each core group (range = 2–60 per group). Then we used POPTOOLS (version 2.7.5, www.cse.csiro.au/poptools) to randomly resample the population-wide observations of mate guarding or copulating (899 observations, involving 147 different males). For each core group, we re-sampled the population-wide data the same number of times we observed mate guarding or copulating in the group (i.e. anywhere from 2 to 60 times), and counted the number of different males that occurred in each re-sample. We replicated this re-sampling procedure 1000 times and used these data to generate a distribution of the number of different males, expected by random chance, to mate guard or copulate in each core group. In order to evaluate significance, we calculated the mean and 95% confidence limits of each random distribution for each core group, and then compared these distributions to the observed number of different males guarding or copulating in each group. In order to test whether females from the same core group had offspring sired by fewer males than expected by chance, we repeated the same procedure as for mate guarding and copulating, but restricted our analysis to the 29 core groups where we assigned paternity for at least two calves, and we randomly sampled from the list of 42 males who sired 152 offspring.

The second simulation tested whether male elephants were more likely to breed in some core groups than others. To do this we, used Monte Carlo randomization simulations to generate a distribution of the number of different core groups in which we expected each male to mate guard, copulate, or sire offspring, given the number of times those events occurred in each core group over the study period. We then compared these random expectations to the

observed number of different core groups where each male guarded, copulated, or sired offspring. Our hypothesis was supported if the observed number of different core groups was less than random expectations. Specifically, we used POPTOOLS to randomly resample the 899 population-wide observations of mate guarding or copulating. For each male, we re-sampled the population-wide data the same number of times we observed him mate guarding or copulating (i.e. anywhere from 2 to 56 times), and counted the number of different core groups that occurred in each re-sample. We replicated this re-sampling procedure 1000 times and used these data to generate a distribution of the number of different core groups we expected each male to be observed mate guarding or copulating. In order to evaluate significance, we calculated the mean and 95% confidence limits of each random distribution for each male, and then compared these distributions to the observed number of different core groups we actually observed males guarding or copulating. In order to test whether males sired offspring with females from fewer core groups than expected by chance, we repeated the same procedure as for mate guarding and copulating, but restricted our analysis to the 29 males who sired at least two calves.

Relatedness within age cohorts. In order to test whether cohorts of paternal relatives occurred across the population, we correlated pairwise genetic relatedness — excluding pairs of animals known to come from the same natal core group — with difference in age in years (N = 526 individuals with known age involved in 149 039 unique pairs). All pairwise genetic relatedness values were estimated using the program KINSHIP (version 1.3.1, Goodnight & Queller 1999), which uses Queller & Goodnight's (1989) relatedness estimator. We previously determined that this was the best kinship estimator for our data (Archie et al. 2007); allele frequencies were based on genotypes for all 545 individuals genotyped from the population. We calculated difference in age as an absolute value by subtracting the birth years of both animals. Pairs whose age difference was zero were born in the same year.

Analyses of population structure. In order to understand how genetic variation was distributed within the study population, we first used Bayesian assignment techniques to test for population structure using the program STRUCTURE (version 2.2, Pritchard et al. 2000). This method identifies clusters of genetically similar individuals from multilocus genotypes without prior knowledge of their genetic relationships. The model assumes K genetic clusters, each characterized by a set of allele frequencies at each locus; the admixture model then probabilistically estimates the proportion of individuals with ancestry in each cluster. We ran a series of pilot runs to estimate $\Pr(X \mid K)$, where X represents the data for K between 1 (the expected value if all individuals belong to the same cluster) and 53 (the number of social groups in the population in 2005). From these initial runs, we determined that we only had power to detect a maximum of about 17 clusters; Ln $\Pr(X \mid K)$ never stabilized even after a Markov chain Monte Carlo (MCMC) burn-in period of 1 million. This lack of power only allowed us to investigate more broad-scale structure, above the level of core social groups. In our final runs to determine the most likely K, we assumed that populations had correlated allele frequencies, inferred alpha from the data, and used a burn-in and MCMC of 200 000 followed by 1 000 000. Longer burn-in or MCMC did not change the results. Because the most likely K was not clearly defined (see results section), we used ΔK to identify the most likely K, according to the method of Evanno et al. (2005).

We also investigated population genetic structure using an analysis of molecular variance (AMOVA), as implemented by ARLEQUIN (version 3.01, Excoffier *et al.* 2005). We confined this analysis to the 195 adult females and 142 calves living in the 21 best genotyped core groups during 2005 (i.e. the year with most complete genotypes, where we genotyped at least three calves and three adult females). For three partitions of the data — all adult females, all adult females and calves, and all calves alone — we determined the degree of correlation among genotypes using hierarchical estimates of Φ, which are analogous to Wright's (1931) *F*-statistics. Specifically, we measured how variation was partitioned between core groups in the population (Φ_{ST}), within individuals relative to the core group (Φ_{IS}), and within individuals relative to the population (Φ_{IT}). We evaluated the significance of these genetic structures using the permutation procedure contained within ARLEQUIN.

We also examined the relationship between average pairwise genetic relatedness within the 21 best genotyped core groups in 2005 and genetic differentiation between core groups in 2005, using linear regression. Average pairwise genetic relatedness among adult females was estimated using KINSHIP software as described above. We estimated genetic differentiation via F_{ST} between all possible pairs of core groups in the population using Weir & Cockerham's (1984) method implemented in GENEPOP (version 3.4; Raymond & Rousset 1995).

Finally, poaching in elephants is age biased, and this is likely to have strong effects on social and genetic structure (Poole 1989a; Ishengoma *et al.* 2007). In order to simulate the effects of age-biased poaching on the genetic structure of core social groups, we repeated our AMOVA analysis on the same data set described above, but excluded all adult females who were over 30 years old and their dependent calves (less than 4 years old). While this estimate is a relatively conservative measure of the effects of poaching — poachers often kill many more than just the oldest

individuals, and it doesn't include the possible change in reproductive patterns with the loss of large old males (Ishengoma *et al.* 2007) — we felt this was a simple way to investigate the effects of age-biased poaching. Poachers often remove the oldest individuals first because they have the largest tusks, and 30 was an appropriate age cut-off as animals over 30 are often conspicuously missing from poached populations (Eltringham & Malpas 1980; Hall-Martin 1980; Poole 1989a; Moss 1990; Barnes & Kapela 1991; Aleper & Moe 2006). For instance, intense poaching in Tarangire National Park, Tanzania, in the late 1970s to the mid 1980s eliminated all males over 30 years old (Moss 1990). In Kidepo Valley National Park, only 18% of individuals were over 25 years old (Aleper & Moe 2006).

Results

Mating behaviour does not increase co-ancestry within core groups of elephants

Average pairwise genetic relatedness within core groups of adult female elephants was 0.15 (Archie *et al.* 2006b). Female matrilocality alone may have been sufficient to generate kinship among female group members. However, elephants may also generate co-ancestry within core social groups if adult females in the same core group breed with a smaller number of males than expected by chance — either through mate choice or coordinated oestrus. In addition, if elephants are like breeding group species, they may also generate co-ancestry within core groups if males sire offspring more often in some core groups than others. However, we found no support for either of these nonrandom patterns of mating behaviour; groups of females were guarded and copulated by the same number of males as expected by random chance, given the number of times each male was observed performing these behaviours across the entire population (Fig. 1). For instance, over the study period, we observed, on average, 16.46 guarding and copulating episodes in each core group (SD = 14.18, median = 12, range = 2–60). On average in each group, 86.86% of these episodes were distributed across different males (SD = 11.82%, median = 86.33%, range = 70% to 100%), and the number of different males almost always fell within the expected confidence limits for each core group, as generated by Monte Carlo simulations (Fig. 1a). Across all core groups, there was no difference between the observed and expected number of males guarding and copulating females in groups (chi-squared test, d.f. = 53, $\chi^2 = 6.29$, $P > 0.5$).

Furthermore, in all 29 social groups where paternity was known for at least two calves, the number of males who sired offspring within each core groups also fit random expectations, given the number of times a given male sired offspring across the population. We assigned

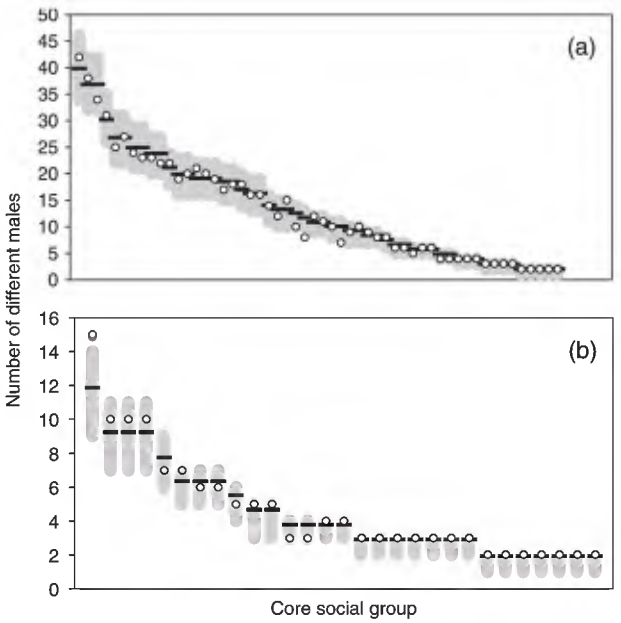

Fig. 1 The observed (open circles) and expected (black bars) number of males who (a) copulated or guarded females from the same core social group, or (b) sired offspring with females from the same core social group. Core social groups are rank-ordered by the expected number of males who engaged in sexual behaviours or sired offspring in each group, as generated by Monte Carlo simulations. Grey bars show the 95% confidence limits for random expectations. Open circles that lie outside these confidence limits indicate social groups who engaged in sexual behaviour or conceived offspring with a larger or smaller number of males than expected by random chance; almost all groups fit random expectations.

paternity to an average of five offspring per core group (SD = 3.44, median = 4, range = 2–15), and on average in each core group, 95.01% of calves were sired by different males (SD = 8.36%, median = 100%, range = 75% to 100%). The number of different males siring offspring in core groups almost always fell within the expected confidence limits, as generated by Monte Carlo simulations (Fig. 1b), and across all social groups, there was no difference between observed and expected number of males siring offspring in groups (chi-squared test, d.f. = 28, $\chi^2 = 1.67$, $P > 0.5$).

Not only did core groups of females not breed with a smaller number of males than expected by chance, but also, males did not breed with a smaller number of core groups than expected by chance. Instead, males guarded, copulated, and sired offspring in the same number of different core social groups as expected by random chance, given the number of times those groups appeared in the data (Fig. 2). For instance, over the study period, each male was observed guarding and copulating, on average, 8.92 times ($N = 95$ males who were observed guarding or copulating at least twice, SD = 9.47, median = 5, range = 2–56). On average

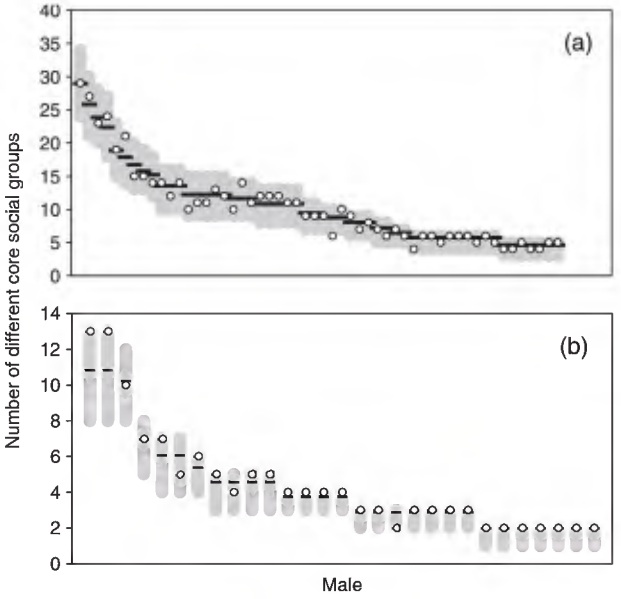

Fig. 2 The observed (open circles) and expected (black bars) number of different core social groups with which each male (a) copulated or guarded females, or (b) sired offspring. Males are rank-ordered by the number core social groups they were expected to engage in sexual behaviours or sired offspring with, as generated by Monte Carlo simulations. Grey bars show the 95% confidence limits for random expectations. Open circles that lie outside these confidence limits indicate males who engaged in sexual behaviour or conceived offspring with a larger or smaller number of core social groups than expected by random chance; almost all males fit random expectations.

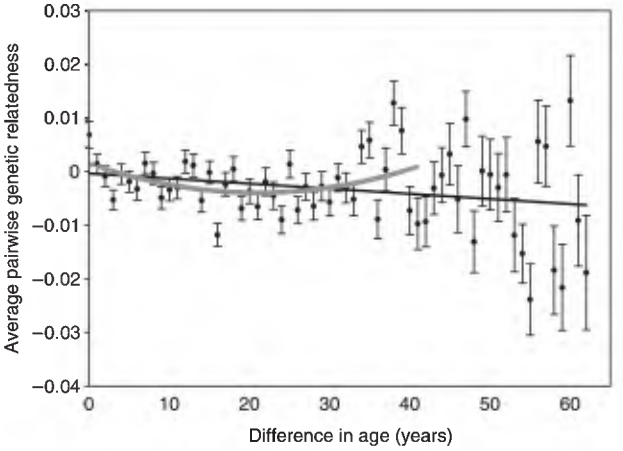

Fig. 3 Average pairwise genetic relatedness among elephants from across the population, as a function of their difference in age in years. Pairs of animals from the same core group are excluded so the relationships in the figure reflect patterns of paternal relatedness across the population. Error bars are standard errors of the mean, black line represents a linear regression of the entire data set; elephants who were closer in age were more closely related (N = 148 807 pairs, r^2 = 0.000042, F = 6.3053, P = 0.0120). The grey line represents a quadratic function fit to pairs of elephants that were no more than 41 years apart in age (i.e. the average age difference between fathers and offspring in our data set; N = 138 825 pairs, r^2 = 0.00015, F = 10.5801, P < 0.0001).

for each male, 88.00% of those guards and copulations were distributed across different core groups (SD = 13.92%, median = 92.31%, range = 51.79% to 100%), and this number of different core groups almost always fell within the expected random confidence limits for each male, as generated by Monte Carlo simulations (Fig. 2a). Across all males, there was no difference between observed and expected number of core groups in which males guarded or copulated females (chi-squared test, d.f. = 94, χ^2 = 8.21, P > 0.5).

Finally, males were not more likely to sire offspring in some core social groups than others. We assigned paternity to an average of 4.83 offspring per male (N = 29 males who sired at least two offspring, SD = 3.47, median = 4, range = 2–14), and on average, 95.46% of each males' calves were sired in different core social groups (SD = 9.49%, median = 100%, range = 71.43% to 100%), and this number of different core groups almost always fell within the expected confidence limits, as generated by Monte Carlo simulations (Fig. 2b). Across all males, there was no difference between observed and expected number of core groups where males sired offspring (chi-squared test, d.f. = 28, χ^2 = 1.88, P > 0.5).

Male-mediated gene flow creates cohorts of paternal relatives across the population

Male elephants sire offspring across multiple social groups, and tend to remain at their peak reproductive success for about 5–10 years, between about 40 or 50 years of age (Hollister-Smith *et al.* 2007). Consequently, we hypothesized that male reproductive peaks would create cohorts of similar-aged paternal relatives across all core groups. In support, pairs of elephants (excluding those from the same core group) who were closer in age were more closely related (Fig. 3; N = 148 807 pairs, r^2 = 0.000042, F = 6.3053, P = 0.0120). While elephants were more closely related to animals in their own age cohort than to those in other cohorts, individuals also appeared to be somewhat more closely related to animals from their fathers' age cohorts (i.e. their fathers and paternal uncles). For instance, the relationships in Fig. 3 suggest the possibility that relatedness was highest among pairs of individuals that were relatively close in age, but was also high among pairs that were 40–50 years apart in age. Indeed, if we limit the regression to pairs of animals that were no more than 41 years apart in age (i.e. the average age difference between fathers and offspring in our data set), the data are better explained by a quadratic function than a linear

Table 1 AMOVA results describing how genetic differentiation is partitioned among 21 core social groups

Source of variation	d.f.	Variance components	Φ	*P*
Adult females only				
Among core groups (Φ_{ST})	20	0.2627	0.0583	< 0.0001
Among individuals within core groups (Φ_{IS})	174	–0.3264	–0.0769	< 0.0001
Within individuals (Φ_{IT})	195	4.5692	– 0.0141	0.9539
Adult females and calves				
Among core groups (Φ_{ST})	20	0.2207	0.0495	< 0.0001
Among individuals within core groups (Φ_{IS})	316	–0.2924	–0.0690	< 0.0001
Within individuals (Φ_{IT})	337	4.5326	–0.0161	0.9924
Calves only				
Among core groups (Φ_{ST})	20	0.0967	0.0264	0.9936
Among individuals within core groups (Φ_{IS})	121	–0.1278	–0.0359	< 0.01
Within individuals (Φ_{IT})	142	3.6901	–0.0085	0.7721
Simulated poaching (no females over 30 years old)				
Among core groups (Φ_{ST})	20	0.1592	0.0359	< 0.0001
Among individuals within core groups (Φ_{IS})	230	–0.2317	–0.0541	< 0.0001
Within individuals (Φ_{IT})	251	4.5116	–0.0163	0.9775

P values were obtained by comparisons of observed values with those generated by random permutation in ARLEQUIN (version 3.01). d.f. represents the degrees of freedom in each analysis. Φ-statistics are analogous to Wright's (1931) *F*-statistics and identify the correlation among alleles at each of the hierarchical levels.

function ($N = 138\,825$ pairs, linear regression $r^2 = 0.00002$, $F = 2.7099$, $P = 0.0997$; quadratic function $r^2 = 0.00015$, $F = 10.5801$, $P < 0.0001$).

Fine-scale genetic structure in elephant populations is age related

A STRUCTURE analysis of the 526 genotyped elephants in Amboseli did not support panmixia; $K = 1$ was the least likely number of distinct genetic clusters; however, STRUCTURE did not reveal striking population genetic differentiation above the level of the core group. The likelihood distribution of *K* increased from $K = 1$ through 3, and then gradually levelled off and plateaued at around $K = 13$. The method of Evanno *et al.* (2005) indicated that the most likely *K* (i.e. *K* with the sharpest change in curvature, or Δ*K*) was 3; however, we could only assign 15% ($N = 69$) of the 526 individuals to any of these three clusters with more than 90% confidence.

Because we did not have enough statistical power to use STRUCTURE to test genetic variation among elephant core social groups, we conducted an AMOVA among the 21 core groups of elephants with the most complete genotypes in 2005 (the year with most complete genotypes). Core social groups of adult females were moderately genetically differentiated; global Φ_{ST} indicated that around 5% or 6% of the variation in allele frequencies was partitioned between core social groups of adult females (with and without their calves) and these fractions were significantly greater than zero (Table 1). This genetic differentiation was driven by co-ancestry among group members. That is, groups of closer kin had higher average pairwise F_{ST} values with the other groups in the population, as compared to groups of less closely related females (linear regression, $r^2 = 0.26$, $F = 144.35$, $P < 0.0001$; Fig. 4). In addition, as is typical of many breeding group populations, fixation indices also reflected unusually high levels of heterozygosity within elephant groups, given their co-ancestry. Global Φ_{IS} among adult females, or adult females and their calves, was significantly less than zero (adult females $\Phi_{IS} = -0.0769$, adult females and calves $\Phi_{IS} = -0.0690$; Table 1).

In breeding group populations, female matrilocality and the fact that males tend to sire more offspring in some social groups than others, create significant genetic differentiation between offspring from different social groups (Pope 1992) — sometimes with more structure between offspring than adults (van Staaden 1995; Dobson *et al.* 1998). In contrast, we did not find significant genetic differentiation among elephant core groups if we only considered the calves living in core social groups in 2005 (age range 0–14 years, average difference in age ± SD = 3.75 ± 2.86); the variation in population allele frequencies among offspring partitioned across social groups was not significantly different than zero (Table 1). This probably occurred because calves that were paternal siblings were distributed across social groups — reflecting substantial male-mediated gene flow between groups — and because most calves living together as immatures were also not maternal siblings; female elephants give birth to a calf once every 4–6 years, and because females mature and male elephants disperse at around age 14, most calves living in the same

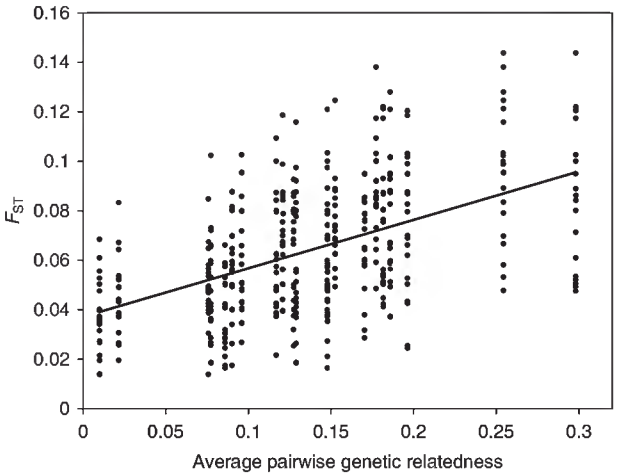

Fig. 4 For 21 different core groups of adult female elephants, the relationship between pairwise genetic differentiation between core groups (F_{ST}; 20 pairwise values for each core group) as a function of the average pairwise genetic relatedness within each core group (a single value for each group). Core groups with higher average pairwise genetic relatedness among adult females were significantly more genetically differentiated from the other core groups in the population (linear regression, $r^2 = 0.26$, $F = 144.35$, $P < 0.0001$).

social group were usually maternal cousins of various degrees. In support, relatedness was lower among calves living as immatures in the same core group at the same time, as compared to adult females living in the same core group at the same time; average pairwise genetic relatedness among calves in the same family was 0.0550 ($N = 458$ pairs, SE = 0.0090), which was significantly less than average pairwise genetic relatedness among adult females in the same family (average $R = 0.1126$, SE ± 0.0063, $N = 931$ pairs; ANOVA, $F = 27.66$, $P < 0.0001$).

Poaching erodes fine-scale genetic structure in elephant populations

In order to understand how age-biased poaching may impact the distribution of genetic variation within populations, we performed an AMOVA on the 21 core groups of females and their calves with the most complete genotypes, but excluded all social group members (i.e. adult females) over 30 years old. This simulated poaching eliminated, on average, the oldest 26% of group members. As expected, it reduced the average pairwise genetic relatedness within and genetic differentiation between core social groups; average pairwise relatedness between the members of 'poached' core groups was 0.0726 (SE ± 0.004, $N = 1594$ pairs), which was significantly lower than the average pairwise genetic relatedness among the members of intact groups (average R in 'unpoached' groups = 0.0937, SE ± 0.0036, $N = 2830$, $F = 12.5318$, $P < 0.001$). Poaching also reduced genetic differentiation between core groups; Φ_{ST} between 'poached' core groups was 0.0359, which was significantly greater than zero, but less than in intact core groups of adult females and calves (Table 1).

Discussion

The fine-scale genetic structure we observed in the Amboseli elephant population was created by patterns of mating and dispersal. Female matrilocality built co-ancestry within core groups and led to significant genetic differentiation between core groups in their entirety, that is, intact lineages of adult female relatives and their calves, whose ages spanned 60 years or more. In addition, gene flow between core groups, mediated most strongly by 40–50 years old males in their reproductive prime, created cohorts of similar-aged paternal relatives in different core groups across the population. This gene flow reduced or erased genetic differences between core groups if we only considered elephants that were around the same age: Φ_{ST} between similar-aged calves from different core social groups was not significantly different than zero. Finally, the age-dependent nature of the fine-scale genetic structure in our study population, combined with the fact that poaching tends to eliminate the oldest elephants from populations, indicates that illegal hunting and poaching will tend to erode fine-scale genetic differences between female social groups in elephant populations.

Fine-scale population genetic structure in elephants and other social mammals

Fine-scale population genetic structure is common in social animals, and among the best-characterized are 'socially structured' or 'breeding group' mammals where matrilocal females form stable social groups and breed with a subset of males that form permanent or semi–permanent associations with female groups (reviewed in Sugg 1996; Storz 1999). Such social organization creates high co-ancestry within social groups, genetic differentiation between groups, and higher than expected heterozygosity among group members. The most extreme examples are found in black-tailed prairie dogs and red howler monkeys where as much as 23% of the genetic variation in populations occurs between social groups (Chesser 1983; Pope 1992; Dobson *et al.* 1998; Pope 1998). However, the majority of breeding group societies have more moderate genetic structure where genetic differentiation between social groups ranges from 4% to 11%. Such species include a number of cercopithecine primates, lions, Richardson's ground squirrels, yellow-bellied marmots, vampire bats, and rabbits (Schwartz *et al.* 1980; Turner 1981; Kawamoto

et al. 1982; Dracopoli *et al.* 1983; Wilkinson 1985; Melnick *et al.* 1986; Melnick 1987; de Jong *et al.* 1994; van Staaden *et al.* 1994; van Staaden 1995; Kawamoto 1996; de Ruiter *et al.* 1998; Surridge *et al.* 1999; Spong *et al.* 2002). Fine-scale genetic structure has also been found in mammals that are not structured into breeding groups (Patton & Feder 1981; McCracken 1987; Cutrera *et al.* 2005; Fredsted *et al.* 2005). Of these, the most relevant to elephants are herd-living ungulates, like sheep and deer (Mathews & Porter 1993; Petit *et al.* 1997; Coltman *et al.* 2003; Nussey *et al.* 2005). In these species, maternal kin do not form stable social groups, but do tend to share overlapping home ranges. Males compete for reproductive dominance over several female ranges, which are clustered into herds or hefts. Genetic differentiation between herds is generally smaller than between breeding groups, and ranges from 0.6% to 4% (Petit *et al.* 1997; Coltman *et al.* 2003; Nussey *et al.* 2005) but see Mathews & Porter (1993).

In elephants, we found that some aspects of genetic structure were similar to that of breeding group species. For instance, we found that 5% to 6% of population-wide genetic variation was structured between core social groups of elephants, which is greater than genetic differences between most ungulate herds and comparable to many breeding group species. This similarity between elephants and breeding group species is probably due to the parallels in their social organization. In elephants as well as breeding group species, female relatives live together in social groups, and this matrilocality creates gene correlations within groups and genetic differentiation between groups. This matrilocality is taken to an extreme in red howler monkeys, whose social groups tend to be small and contain a single, closely related matriline (Pope 1992; Pope 1998). However, female elephants and most breeding group species — especially cercopithecine primates — tend to live in larger social groups with multiple matrilines, so that not all group members are necessarily closely related (e.g. de Ruiter *et al.* 1998; Archie *et al.* 2006b). In comparison, genetic differences between ungulate herds are usually less than between breeding or elephant groups partly because female matrilocality is not as strict and ungulate herds are larger and hence tend to encompass more of the population's genetic variation (Mathews *et al.* 1993; Petit *et al.* 1997; Coltman *et al.* 2003; Nussey *et al.* 2005).

On other measures, elephants were quite different from breeding groups. In breeding group species, paternal kinship can create gene correlations within groups, and genetic differentiation between groups, as males form permanent or semi-permanent breeding associations with one or a few female groups. In the most extreme cases, female group members breed almost exclusively with a single, long-tenured male (Chesser 1983; Pope 1992; Dobson *et al.* 1998; Pope 1998), although in most breeding group species, females breed with multiple males (e.g. Melnick 1987). In contrast, in both elephants and herd-living ungulates, rates of male-mediated gene flow between groups are probably almost always higher than in breeding group species (Poole 1986; Poole 1989b; Poole & Moss 1989; Coltman *et al.* 2003; Nussey *et al.* 2005; Hollister-Smith *et al.* 2007). The extent to which this more fluid mating system generates fine-scale genetic structure within populations depends partly on demography and population density. For instance, in red deer, a release from hunting led to a more even distribution of mating opportunities across the population, and fine-scale genetic differences between herds consequently declined from 4% to nearly 1% (Nussey *et al.* 2005). However, in elephants we did not find evidence that nonrandom mating behaviour increased gene correlations within groups and genetic differences between groups — at least on the scale of female groups living in and around Amboseli National Park.

Elephants also appear to differ from breeding group species in that the fine-scale population genetic structure we observed was age dependent. That is, the degree of differentiation across social groups depended upon the age difference between the individuals involved; genetic differentiation among animals more similar in age, from different core groups, was less than between intact social groups. This age-dependent fine-scale genetic structure seems to be a consequence of the fact that, in natural and intact elephant populations, males sire offspring across multiple core groups of females and tend to do so during an extended high-fertility period in their 40s and 50s (Hollister-Smith *et al.* 2007). This age-dependence at the level of the entire population differs from many breeding group species, where offspring living in the same group are significantly genetically differentiated from those in other groups (Pope 1992; van Staaden 1995; Dobson *et al.* 1998; Pope 1998). In breeding group species, genetic structure among offspring is partly due to female matrilocality, but also to permanent or semi–permanent associations between males and female social groups, which create gene correlations among offspring from the same group and genetic differentiation between groups. We hypothesize that age-dependent genetic structure may occur in other long-lived species where males wait in a queue to reproduce and breed across the population, including sperm whales, perhaps other cetaceans, or ungulates where males have a discrete period of reproductive dominance and sire multiple offspring across many female ranges.

Evolutionary and conservation genetic implications of elephant genetic structure

Fine-scale genetic structure within elephant populations has at least three potentially important consequences. It

may (i) determine opportunities for kin selection, (ii) intensify founder effects if populations are fragmented, and (iii) influence the rate at which genetic diversity is lost from populations through genetic drift. Of these, the opportunities for kin selection are best understood — especially for adult female elephants (Dublin 1983; Moss & Poole 1983; Lee 1987; Moss 1988; Archie *et al.* 2006a, b). Kin selection has the potential to influence female relationships, as adult females living in the same core social group are moderately closely related and females spend most of their lives together with their first-order maternal relatives (Archie *et al.* 2006b). The results we present here confirm our hypotheses about patterns of paternal relatedness in elephant populations. Because males reach their peak reproductive success between 40 and 50 years of age and tend to sire offspring in multiple social groups across the population (Hollister-Smith *et al.* 2007), an individual's closest paternal relatives tend to be distributed across social groups in the population, and tend to be similarly aged paternal siblings or paternal aunts and uncles from their father's age cohort. It is unknown whether elephants form special relationships with their paternal kin; however, at the very least, elephants appear to be able to recognize and avoid inbreeding with their paternal relatives (Archie *et al.* 2007). One set of relationships where paternal kinship may be most likely to play a role, because these relationships involve interactions between individuals from several social groups, are nonrandom associations between male elephants. Because maternal, and possibly paternal, kinship is an important component of elephant social relationships, conservation strategists and managers should strive to keep natural elephant social organization intact (Slotow *et al.* 2000; Nyakaana *et al.* 2001; Bradshaw *et al.* 2005).

In addition to determining opportunities for kin selection, fine-scale genetic structure — especially the genetic differences between core social groups — has the potential to intensify founder effects (Templeton 1980; Storz 1999). For instance, if a single social group colonizes new habitat, the allele frequencies in that group will probably not accurately reflect allele frequencies in the group's original population. This genetic structure may intensify the evolutionary change that occurs as a result of the founding event (Templeton 1980; Storz 1999). Emigration of whole core groups of females is probably unusual in natural populations of elephants, as genetic evidence suggests that gene flow between populations is male biased (Nyakaana & Arctander 1999). However, in Amboseli, at least one core social group is thought to be a migrant from a neighbouring population, as the members of this group all share a haplotype that is unique in Amboseli but shared with elephants in northern Kenya (EA Archie, CL Fitzpatrick, CJ Moss, SC Alberts, unpublished). In addition, fine scale genetic structure in elephant populations has important implications for conservation, as translocations of wild elephants risk creating populations with low genetic diversity that do not necessarily reflect the genetic structure of a natural elephant population.

Finally, fine-scale genetic structure in elephant populations may influence the loss of genetic variation due to genetic drift. When population geneticists first considered the genetic structure of social species, many assumed that the division of populations into genetically distinct social groups accelerated the loss of genetic diversity (Bush *et al.* 1977; Baker *et al.* 1980; Templeton 1980). This was because social groups were thought to act like small populations where alleles were lost rapidly due to inbreeding and genetic drift. However, this is not the case and instead, inbreeding is usually prevented by sex-biased dispersal, and F_{IS} within social groups is almost always negative (Melnick 1987; Sugg 1996; Storz 1999). Hence, an alternative view is that breeding group structure actually slows the loss of genetic diversity from populations (Chesser *et al.* 1993; Sugg 1994; Sugg 1996). In support, the effective population size of breeding group populations may sometimes be larger than the census size (Chesser *et al.* 1993; Sugg 1994; Sugg 1996), and if genetic substructure decreases, genetic diversity may be lost from populations (Dobson *et al.* 2004). For instance, if genetic differences between social groups were lost, then the risk of losing alleles due to genetic drift would increase (Dobson *et al.* 2004). This result is especially relevant for elephants, as illegal hunting erodes fine-scale genetic structure in elephant populations. In poached populations, older animals are lost and natural social groups are destroyed — both of which lead to smaller, less genetically structured populations. Hence, it is possible for genetic diversity to be lost from poached populations more rapidly than from intact populations — even if those populations have equal census sizes. Perhaps more important is the loss of large, and therefore old, breeding males, which may reduce genetic diversity by increasing the reproductive tenure of younger males (Poole 1989a; Ishengoma *et al.* 2007). Illegal elephant hunting and limited trade in ivory is increasing in Africa, despite the ivory ban (Stiles & Martin 2001; Martin 2005; Wasser *et al.* 2007); our results would strongly support conservation efforts that reduce poaching and keep elephant social organization intact.

Acknowledgements

We thank the Office of the President of Kenya for permission to work in Amboseli National Park under permit number MOES & T 13/001/30C 72/7. We thank the Kenya Wildlife Service for local sponsorship. We thank the Amboseli Elephant Research project for invaluable scientific and logistical support, particularly the team of N. Njiraini, K. Sayialel and S. Sayialel who contributed greatly to the collection of genetic and behavioural data. This research was supported by the Smithsonian Institution, Friends of

the National Zoo, the National Science Foundation (IBN0091612 to SCA), the Amboseli Trust for Elephants, the Amboseli Elephant Research Project, and Duke University.

References

Aleper D, Moe SR (2006) The African savannah elephant population in Kidepo Valley National Park, Uganda: changes in size and structure from 1967 to 2000. *African Journal of Ecology*, **44**, 157–164.

Archie EA, Moss CJ, Alberts SC (2003) Characterization of tetranucleotide microsatellite loci in the African savannah elephant (*Loxodonta africana africana*). *Molecular Ecology Notes*, **3**, 244–246.

Archie EA, Morrison TA, Foley CAH, Moss CJ, Alberts SC (2006a) Dominance rank relationships among wild female African elephants (*Loxodonta africana*). *Animal Behaviour*, **71**, 117–127.

Archie EA, Moss CJ, Alberts SC (2006b) The ties that bind: genetic relatedness predicts the fission and fusion of groups in wild African elephants (*Loxodonta africana*). *Proceedings of the Royal Society B: Biological Sciences*, **273**, 513–522.

Archie EA, Hollister-Smith JA, Poole JH *et al.* (2007) Behavioral inbreeding avoidance in wild African elephants. *Molecular Ecology*, **16**, 4138–4148.

Baker MC, Marler P (1980) Behavioral adaptations that constrain the gene pool in vertebrates. In: *Evolution of Social Behavior: Hypotheses and Empirical Tests* (ed Markl H), pp. 59–80. Verlag Chemic, Weinheim, Germany.

Barnes RFW, Kapela EB (1991) Changes in the Ruaha elephant population caused by poaching. *African Journal of Ecology*, **29**, 289–294.

Bradshaw GA, Schore AN, Brown JL, Poole JH, Moss CJ (2005) Elephant breakdown. *Nature*, **433**, 807.

Bush GL, Case M, Wilson AC, Patton J (1977) Rapid speciation and chromosomal evolution in mammals. *Proceedings of the National Academy of Sciences, USA*, **74**, 3942–3946.

Chesser RK (1983) Genetic variability within and among populations of the black-tailed prairie dog. *Evolution*, **37**, 320–331.

Chesser RK (1991a) Gene diversity and female philopatry. *Genetics*, **127**, 437–447.

Chesser RK (1991b) Influence of gene flow and breeding tactics on gene diversity within populations. *Genetics*, **129**, 573–583.

Chesser RK, Rhodes OE, Sugg DW, Schnabel A (1993) Effective sizes for subdivided populations. *Genetics*, **135**, 1221–1232.

Christal J, Whitehead H (2001) Social affiliations within sperm whale (*Physeter macrocephalus*) groups. *Ethology*, **107**, 323–340.

Coltman DW, Pilkington JG, Pemberton JM (2003) Fine-scale population genetic structure in a free-living ungulate population. *Molecular Ecology*, **12**, 733–742.

Cutrera AP, Lacey EA, Busch C (2005) Genetic structure in a solitary rodent (*Ctenomys talarum*): implications for kinship and dispersal. *Molecular Ecology*, **14**, 2511–2523.

Dobson FS, Chesser RK, Hooglang JL, Sugg DW, Foltz DW (1997) Do black-tailed prairie dogs minimize inbreeding? *Evolution*, **51**, 970–978.

Dobson FS, Chesser RK, Hooglang JL, Sugg DW, Foltz DW (1998) Breeding groups and gene dynamics in a socially structured population of prairie dogs. *Journal of Mammalogy*, **79**, 671–680.

Dobson FS, Chesser RK, Hooglang JL, Sugg DW, Foltz DW (2004) The influence if social breeding groups on effective population size in black-tailed prairie dogs. *Journal of Mammalogy*, **85**, 58–66.

Douglas-Hamilton I (1972) *On the Ecology and Behaviour of the African Elephant: the Elephants of Manyara Dphil.* Oxford University, Oxford, UK.

Dracopoli NC, Brett FL, Turner TR, Jolly CJ (1983) Patterns of genetic variability in the serum proteins of the Kenyan vervet monkey (*Cercopithicus aethiops*). *American Journal of Physical Anthropology*, **61**, 39–49.

Dublin HT (1983) Cooperation and reproductive competition among female African elephants. *Social Behavior of Female Vertebrates* (ed. Wasser SK), pp. 291–313. Academic Press, New York.

Eltringham SK, Malpas RC (1980) The decline in elephant numbers in Rwenzori and Kabalega Falls National Parks, Uganda. *African Journal of Ecology*, **18**, 73–86.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

Ewens WJ, Spielman RS (1995) The transmission disequilibrium test — history, subdivision and admixture. *American Journal of Human Genetics*, **57**, 455–464.

Excoffier L, Laval G, Schneider S (2005) ARLEQUIN version 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

Fredsted T, Pertoldi C, Schierup MH, Kappeler PM (2005) Microsatellite analyses reveal fine-scale genetic structure in grey mouse lemurs (*Microcebus murinus*). *Molecular Ecology*, **14**, 2363–2372.

Goodnight KF, Queller DC (1999) Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology*, **8**, 1231–1234.

Hall-Martin AJ (1980) Elephant survivors. *Oryx*, **15**, 355–362.

Haynes G (1991) Mammoths, mastodons, and elephants: *Biology, Behavior, and the Fossil Record*. Cambridge University Press, New York.

Hazlitt SL, Eldridge MDB, Goldizen AW (2004) Fine-scale spatial genetic correlation analyses reveal strong female philopatry within a brush-tailed rock-wallaby colony in southeast Queensland. *Molecular Ecology*, **13**, 3621–3632.

Hazlitt SL, Sigg DP, Eldridge MDB, Goldizen AW (2006) Restricted mating dispersal and strong breeding group structure in a mid-sized marsupial mammal (*Petrogale penicillata*). *Molecular Ecology*, **15**, 2997–3007.

Höglund J, Shorey L (2003) Local genetic structure in a white-bearded manakin population. *Molecular Ecology*, **12**, 2457–2463.

Hollister-Smith JA, Poole JH, Archie EA *et al.* (2007) Age, musth and paternity in wild male African elephants, *Loxodonta africana*. *Animal Behaviour*, **74**, 287–296.

Ishengoma DRS, Shedlock AM, Foley CAH *et al.* (2007) Effects of poaching on bull mating success in a free ranging African elephant (*Loxodonta Africana*) population of Tarangire National Park, Tanzania. *Conservation Genetics*, DOI: 10.1007/s10592-007-9332-0.

de Jong G, de Ruiter JR, Haring R (1994) *Genetic Structure of a Population with Social Structure and Migration*. Birkhauser-Verlag, Basel.

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1006.

Kawamoto Y (1996) Population genetic study of Sulawesi macaques. In: *Variation in the Asian Macaques* (eds Shotake T, Wada K), pp. 37–65. Tokyo University Press, Tokyo, Japan.

Kawamoto Y, Ischak TM, Supriatna J (1982) Gene constitution of crab-eating macaques (*Macaca fascicularis*) on Lombok and Sumbawa. *Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates*, **2**, 57–64.

Krutzen M, Barre LM, Connor RC, Mann J, Sherwin WB (2004) 'O father: where art thou?' — Paternity assessment in an open fission-fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Molecular Ecology*, **13**, 1975–1990.

Lee PC (1987) Allomothering among African elephants. *Animal Behaviour*, **35**, 278–291.

Lee PC, Moss CJ (1995) Statural growth in known-age African elephants (*Loxodonta africana*). *Journal of Zoology*, **236**, 29–41.

Lindeque M, van Jaarsveld AS (1993) Post-natal growth of elephants *Loxodonta africana* in Etosha National Park, Namibia. *Journal of Zoology*, **229**, 319–330.

Martin E (2005) Northern Sudan ivory market flourishes. *Pachyderm*, **39**, 67–76.

Mathews NE, Porter WF (1993) Effect of social structure on genetic structure of free ranging white-tailed deer in the Adirondack mountains. *Journal of Mammalogy*, **74**, 33–43.

McCracken GF (1987) Genetic structure of bat social groups. In: *Recent Advances in the Study of Bats* (eds Fenton MB, Racey PA, Rayner JMV), pp. 281–298. Cambridge University Press, Cambridge, UK.

Melnick DJ (1987) The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. *Genetica*, **73**, 117–135.

Melnick D, Pearl M (1986) Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (ed. Smuts B), pp. 121–134. The University of Chicago Press, Chicago.

Melnick D, Pearl M, Richard AF (1984) Male migration and inbreeding avoidance in wild rhesus monkeys. *American Journal of Primatology*, **7**, 229–243.

Morrison TA, Chiyo PI, Moss CJ, Alberts SC (2005) Measures of dung bolus size for known-age African elephants (*Loxodonta africana*): implications for age estimation. *Journal of Zoology*, **266**, 89–94.

Moss CJ (1983) Oestrous behaviour and female choice in the African elephant. *Behaviour*, **86**, 167–196.

Moss CJ (1988) *Elephant Memories*. University of Chicago Press, Chicago.

Moss CJ (1990) Elephants in Tarangire. *Pachyderm*, **13**, 26–30.

Moss CJ (2001) The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology*, **255**, 145–156.

Moss CJ, Poole JH (1983) Relationships and social structure of African elephants. In: *Primate Social Relationships* (ed. Hinde RA), pp. 315–325. Sinauer & Associates, Sunderland, Massachusetts.

Nussey DH, Coltman DW, Coulson TN *et al.* (2005) Rapidly declining fine-scale spatial genetic structure in female red deer. *Molecular Ecology*, **14**, 3395–3405.

Nyakaana S, Arctander P (1998) Isolation and characterization of microsatellite loci in the African elephant, *Loxodonta africana*. *Molecular Ecology*, **7**, 1431–1439.

Nyakaana S, Arctander P (1999) Population genetic structure of the African elephant in Uganda based on variation at mitochondrial and nuclear loci: evidence for male biased gene flow. *Molecular Ecology*, **8**, 1105–1115.

Nyakaana S, Abe EL, Arctander P, Siegismund HR (2001) DNA evidence for elephant social breakdown in Queen Elizabeth National Park, Uganda. *Animal Conservation*, **4**, 231–237.

Patton JL, Feder JH (1981) Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. *Evolution*, **35**, 912–920.

Petit E, Aulagnier S, Bon R, Dubois M, Crouay-Roy B (1997) Genetic structure of populations of the Mediterranean mouflon (*Ovis gmelini*). *Journal of Mammalogy*, **78**, 459–467.

Poole JH (1986) Rutting behavior in African elephants: the phenomenon of musth. *Behaviour*, **102**, 283–316.

Poole J (1989a) The effects of poaching on the age structures and social and reproductive patterns of selected east African elephant populations. In: *The Ivory Trade and the Future of the African Elephant*. The Ivory Trade Review Group, prepared for the 7th CITES conference of the parties.

Poole JH (1989b) Mate guarding, reproductive success and female choice in African elephants. *Animal Behaviour*, **37**, 842–849.

Poole JH, Moss CJ (1989) Elephant mate searching: group dynamics and vocal and olfactory communication. In: *The Biology of Large African Mammals in Their Environment* (eds Jewell PA, Maloiy GMO), pp. 111–125. Clarendon Press, Oxford, UK.

Pope TR (1992) The influence of dispersal patterns and mating system of genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). *Evolution*, **46**, 1112–1128.

Pope TR (1998) Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. *Journal of Mammalogy*, **79**, 692–712.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Rossiter SJ, Ransome RD, Faulkes CG, Le Comber SC, Jones G (2005) Mate fidelity and intra-lineage polygyny in greater horseshoe bats. *Nature*, **437**, 408–411.

de Ruiter J, Geffen E (1998) Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). *Proceedings of the Royal Society B: Biological Sciences*, **265**, 79–87.

Schwartz O, Armitage K (1980) Genetic variation in social mammals: the marmot model. *Science*, **207**, 665–667.

Slotow R, van Dyk G, Poole J, Page B, Klocke A (2000) Older bull elephants control young males. *Nature*, **408**, 425–426.

Spong G, Stone J, Creel S, Bjorkland M (2002) Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. *Journal of Evolutionary Biology*, **15**, 945–953.

van Staaden MJ (1995) Breeding tactics, social structure and genetic variation in mammals: problems and prospects. *Acta Theriologica, Suppl*, **3**, 165–182.

van Staaden M, Chesser R, Michener G (1994) Genetics correlations and matrilineal structure in a population of Spermophilus richardsonii. *Journal of Mammalogy*, **75**, 573–582.

van Staaden MJ, Michener GR, Chesser RK (1996) Spatial analysis of microgeographic structure in Richardson's ground squirrels. *Canadian Journal of Zoology*, **74**, 1187–1195.

Stiles D, Martin E (2001) Status and trends of the ivory trade. *Pachyderm*, **30**, 24–36.

Storz J (1999) Genetic consequences of mammalian social structure. *Journal of Mammalogy*, **80**, 553–569.

Storz JF (2005) Nonrandom dispersal and local adaptation. *Heredity*, **95**, 3–4.

Sugg DWC, R (1994) Effective population sizes with multiple paternity. *Genetics*, **137**, 1147–1155.

Sugg DWCR, Dobson FS, Hooglang JL (1996) Population genetics meets behavioral ecology. *Trends in Ecology & Evolution*, **11**, 338–342.

Surridge AK, Ibrahim KM, Bell DJ *et al.* (1999) Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). *Molecular Ecology*, **8**, 299–307.

Taberlet P, Griffin S, Goossens B *et al.* (1996) Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research*, **24**, 3189–3194.

Templeton AR (1980) The theory of speciation via the founder principle. *Genetics*, **94**, 1011–1038.

Turner TR (1981) Blood protein variation in a population of Ethiopian vervet monkeys (*Cercopithecus aethiops*). *American Journal of Physical Anthropology*, **55**, 225–232.

Wasser SK, Mailand C, Booth R *et al.* (2007) Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proceedings of the National Academy of Sciences, USA*, **104**, 4228–4233.

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

Whitehead H (1996) Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, **38**, 237–244.

Whitehead H (2003) *Social Evolution in the Ocean*. University of Chicago Press, Chicago.

Whitehead H, Waters S, Lyrholm T (1991) Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behavioral Ecology and Sociobiology*, **29**, 385–389.

Wilkinson G (1985) The social organization of the common vampire bat. *Behavioral Ecology and Sociobiology*, **17**, 123–134.

Wittemyer G, Douglas-Hamilton I, Getz WM (2005) The socioecology of elephants: analysis of the processes creating multitired social structures. *Animal Behaviour*, **69**, 1357–1371.

Woxvold IA, Adcock GJ, Mulder RA (2006) Fine-scale genetic structure and dispersal in cooperatively breeding apostlebirds. *Molecular Ecology*, **15**, 3139–3146.

Wright SW (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–159.

Wright S (1965) The interpretation of population structure by *F*-statistics with special regard to systems of mating. *Evolution*, **19**, 395–420.

Elizabeth Archie studies the evolution of social behaviour and its genetic causes and consequences. Jésus Maldonado is interested in using molecular genetic tools to answer basic and applied questions dealing with conservation genetics, systematics, behavioural ecology and the evolution and genetic diversity of a variety of mammals. Julie Hollister-Smith is interested in reproductive behaviour and chemical communication. Joyce Poole studies elephant social and sexual behaviour and communication. Cynthia Moss has spent more than 30 years in Africa studying elephants and working for their conservation. Rob Fleischer is head of the Center for Conservation and Evolutionary Genetics at the Smithsonian's National Zoo and has research interests in evolutionary biology and in the application of genetic markers to conservation, population and systematic studies of birds and mammals. Susan Alberts studies demographic, environmental, and genetic correlates of and sources of variance in fitness components in natural population of large mammals, particularly African elephants and baboons.
