INVITED REVIEW

Elephant behaviour and conservation: social relationships, the effects of poaching, and genetic tools for management

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Abstract

Genetic tools are increasingly valuable for understanding the behaviour, evolution, and conservation of social species. In African elephants, for instance, genetic data provide basic information on the population genetic causes and consequences of social behaviour, and how human activities alter elephants' social and genetic structures. As such, African elephants provide a useful case study to understand the relationships between social behaviour and population genetic structure in a conservation framework. Here, we review three areas where genetic methods have made important contributions to elephant behavioural ecology and conservation: (1) understanding kin-based relationships in females and the effects of poaching on the adaptive value of elephant relationships, (2) understanding patterns of paternity in elephants and how poaching can alter these patterns, and (3) conservation genetic tools to census elusive populations, track ivory, and understand the behavioural ecology of crop-raiding. By comparing studies from populations that have experienced a range of poaching intensities, we find that human activities have a large effect on elephant behaviour and genetic structure. Poaching disrupts kin-based association patterns, decreases the quality of elephant social relationships, and increases male reproductive skew, with important consequences for population health and the maintenance of genetic diversity. In addition, we find that genetic tools to census populations or gather forensic information are almost always more accurate than non-genetic alternatives. These results contribute to a growing understanding of poaching on animal behaviour, and how genetic tools can be used to understand and conserve social species.

Key words: animal mating/breeding systems, behaviour/social evolution, conservation genetics, wildlife management

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Introduction

Genetic tools are critical for understanding the behaviour, evolution, and conservation of social animals. For instance, behavioural ecologists commonly use patterns of genetic variation to reveal patterns of breeding, dispersal, and cooperation, which would otherwise be difficult to uncover using behavioural observations alone (e.g. Burke *et al.* 1989; Buchan *et al.* 2003; Hall *et al.* 2009). Furthermore, these patterns of breeding,

dispersal, and social association create distinctive patterns of genetic variation in social species, with important evolutionary consequences (e.g. Bush *et al.* 1977; Storz 1999; Ross 2001; Charpentier *et al.* in press). In terms of species conservation, genetic tools contribute key information to managers and conservation biologists about population size, disturbance or forensics (e.g. Alter *et al.* 2007; Lowenstein *et al.* 2009; Banks *et al.* in press). Finally, many conservation problems—from habitat fragmentation to illegal hunting—disrupt or destroy animal societies. In turn, these disruptions can limit the adaptive value of animal social relationships or alter the structure of genetic variation

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in animal populations (Coltman *et al.* 2003; Goossens *et al.* 2006; Williams & Lusseau 2006; Milner *et al.* 2007).

In African elephants, genetic tools have been used for nearly all of these purposes—to provide basic information to managers, to understand the population genetic causes and consequences of social behaviour, and to learn how poaching alters elephants' social and genetic structures (e.g. Nyakaana *et al.* 2001; Archie *et al.* 2006; Wasser *et al.* 2007; Wittemyer *et al.* 2009). As such, African elephants are a useful case study for understanding the relationships between social behaviour and population genetic structure in a conservation framework.

Moreover, African elephants are an especially interesting system for addressing these questions for two reasons. First, elephants are of great conservation concern. In the 1970s and 1980s, poaching reduced wild African elephant populations from 1.3 million animals to 600 000 in less than a decade (Douglas-Hamilton 1987; Cumming *et al.* 1990). This illegal hunting selectively removed older animals with large tusks (Poole 1989a), and we are just now beginning to understand the consequences of these effects for elephant societies and genetic structure (Fig. 1; Slotow *et al.* 2000; Gobush *et al.* 2008; Ishengoma *et al.* 2008). Unfortunately, poaching is again on the rise in a number of elephant populations (Wasser *et al.* 2007, 2010; Douglas-Hamilton 2008; Dunham 2008). Wild elephants are also facing new threats from habitat fragmentation and human-wildlife conflict, as elephant populations are increasingly constrained to live in smaller areas with growing contact with humans and livestock. Hence, understanding how elephant social behaviour shapes and is shaped by genetic structure, and how humans are changing those relationships, is necessary to conserve wild elephants.

Second, elephants are interesting because their societies differ from other social mammals in several important ways, with consequences for population genetics and evolution. For instance, unlike many social mammals, where individuals live in stable social groups, elephants live in fluid, fission–fusion societies where the composition of group members changes over the course of hours, days or seasons (Moss & Poole 1983; Wittemyer *et al.* 2005). The flexible nature of these societies is thought to allow individuals to respond adaptively to changing resources or threats by altering the number and identity of animals with which they associate. This system is shared with only a few other highly social species, including chimpanzees, humans, a few other primates, some bats, carnivores and cetaceans (White 1992; Holekamp *et al.* 1997; Kerth & Konig 1999; Connor 2004). In fission–fusion societies, it might be more difficult for genetic relatives to find each other and interact, with consequences for the evolution of social behaviour (Archie *et al.* 2006, 2008; Wittemyer *et al.* 2009). Furthermore, because female elephants are a highly mobile, scarce resource, male elephants appear to experience intense intra-sexual competition for mates, leading to unusual patterns of paternity (Hollister-Smith *et al.* 2007; Rasmussen *et al.* 2008). Finally, unlike many male mammals, male elephants breed with females from across the entire population. Hence, there are more opportunities for inbreeding because males can return and breed in their natal social group, and paternal kin might occur in several groups (Archie *et al.* 2007, 2008).

Here, we review genetic contributions to understanding the behaviour, evolution and conservation of elephants. While elephants face several important conservation issues, we restrict our review to human impacts, especially poaching, on elephant societies, population genetics, and conservation. Specifically, we review three areas. First, we explore whether kinship predicts the strength of elephant social relationships, and how poaching changes the strength and quality of these relationships. Second, we examine which factors predict patterns of male reproductive success and inbreeding avoidance, and how poaching changes these patterns. Third, we assess the utility of genetic tools for elephant conservation and management. We conclude with a discussion of future directions for research on the population and conservation genetic causes and consequences of behaviour.
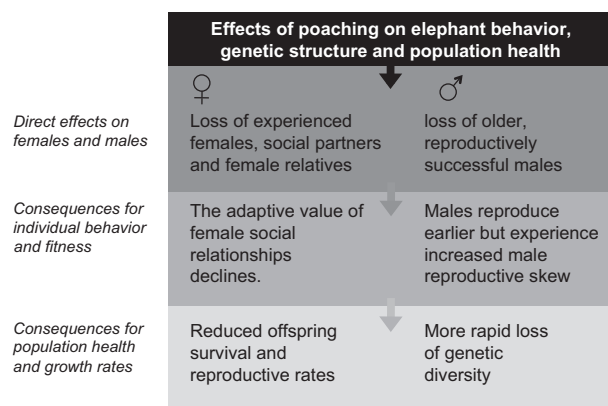

Effects of poaching on elephant behavior, genetic structure and population health		
	♀	♂
Direct effects on females and males	Loss of experienced females, social partners and female relatives	loss of older, reproductively successful males
Consequences for individual behavior and fitness	The adaptive value of female social relationships declines.	Males reproduce earlier but experience increased male reproductive skew
Consequences for population health and growth rates	Reduced offspring survival and reproductive rates	More rapid loss of genetic diversity

Fig. 1 Proposed effects of poaching on elephant social relationships, fitness, and population health, as reviewed in this paper. Specifically, poaching removes older animals and kin from elephant populations, with important consequences for females and males. For females, the loss of important social partners may decrease female fitness, which may influence population growth rates. For males, poaching seems to increase reproductive skew, which may increase the rate at which genetic diversity is lost from natural populations.

Kinship, elephant social relationships, and the impact of poaching

Kinship is often an important predictor of the strength and quality of social bonds; for instance, in many social mammals, females live together in stable groups and form cooperative relationships with their female relatives. These relationships are often fundamentally stronger and more beneficial than relationships with non-kin (e.g. Rossiter *et al.* 2002; Silk *et al.* 2006; Perry *et al.* 2008). Indeed, relationships between close kin can increase female fitness, and if related social partners are removed from populations, their absence can reduce the adaptive value of female social relationships (e.g. Pusenius *et al.* 1998; Silk *et al.* 2003; Milner *et al.* 2007). However, in fission–fusion societies, where group composition can change over the course of hours, weeks, or seasons, relatives might not always remain together. If so, cooperative relationships might form among non-kin as well as kin, and the loss of kin per say, as opposed to any close social partner, might not affect female fitness. Here, we review evidence that elephants form close and enduring social relationships with kin (e.g. Archie *et al.* 2006; Chiyo *et al.* 2011a). We then discuss how poaching disrupts kin structure in elephant societies, and whether this situation limits the benefits of elephant social relationships (e.g. Gobush *et al.* 2008; Wittemyer *et al.* 2009).

In elephants, individuals have the opportunity to interact with almost any other member of the population over the course of a year (Douglas-Hamilton 1972; Moss & Poole 1983). This pattern is illustrated by the social networks in Fig. 2, which show patterns of social
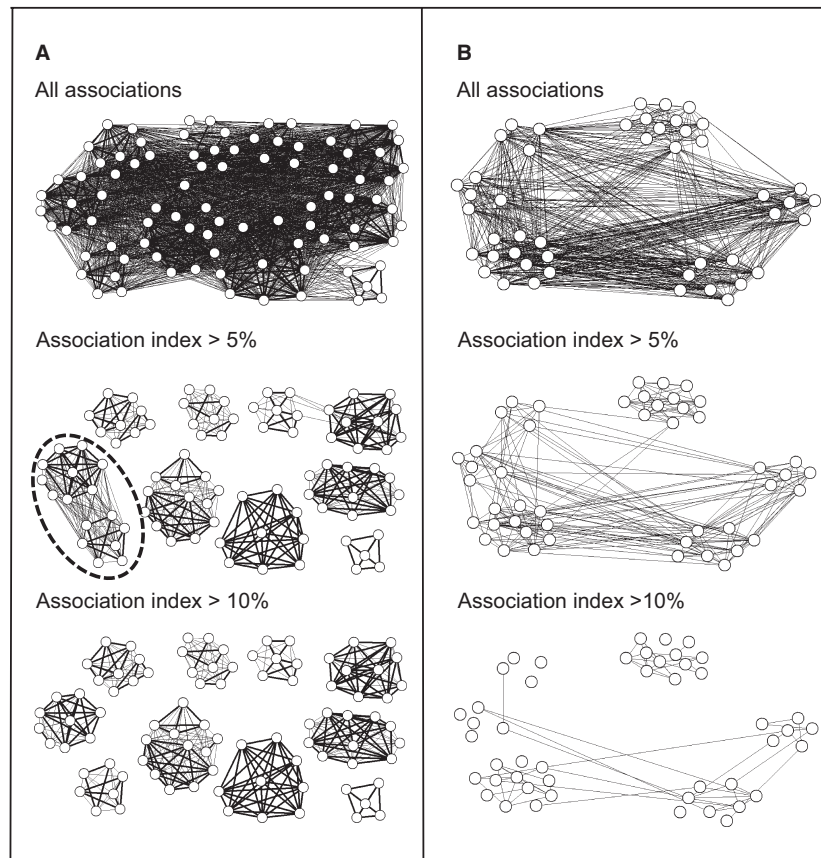

Fig. 2 Social networks illustrate variation in the patterns of social association between (A) female (B) and male African elephants living in Amboseli National Park, Kenya. Data to construct networks were derived from 1,240 observations of 89 female elephants and 939 observations of 47 male elephants collected over three years. *Circles* represent individual elephants (nodes), and the lines that link nodes depict the percent of time individuals spent together in the same group. We present three networks each for male and female associates; the *top row* of networks includes all observed associations, the *second row* only shows associations between animals that spent more than 5% of their time in the same group, while the *bottom row* shows associations between animals that spent more than 10% of their time in the same group. *Thin black lines* occur between individuals that spent greater than 0% but less than 50% of their time together in the same group. *Thick black lines* occur between pairs of animals that more than 50% of their time together in the same group. The ten clusters in the 10% association figure for females indicate core social groups. The *dashed circle* in the 5% association figure for females indicates a bond group.

Table 1 Effects of poaching on kin-based social associations in five African elephant populations

Population	Percent population decline due to poaching	Percent of core groups with uniformity of mtDNA haplotypes	Percent of bond groups with uniformity of mtDNA haplotypes	Percent of core groups where relatedness is significantly greater than zero	Correlation between genetic relatedness and female associations (P value)	Sources
Amboseli National Park, Kenya	30%	95% (37 of 39)	89% (8 of 9)	80% (8 of 10)	0.31 (<0.0001)	Archie *et al.* (2006)
Mikumi National Park, Tanzania	75%	–	–	54% (20 of 37)	0.09 (<0.001)	Gobush *et al.* (2009)
Samburu National Reserve, Kenya	85%	91% (21 of 23)	75% (9 of 12)	79% (23 of 29)	0.25 (<0.001)	Wittemyer *et al.* (2009)
Sengwa Wildlife Research Area, Zimbabwe	82%	–	25% (1 of 4)	–	–	Charif *et al.* (2005)
Queen Elizabeth National Park, Uganda	96%	67% (6 of 9)	–	–	–	Nyakaana *et al.* (2001)

association for female (A) and male (B) elephants over three years in Amboseli National Park, Kenya. The ten clusters at the bottom of Fig. 2a depict associations within ten ''core'' groups of elephants. Core groups are a fundamental unit of female relationships and are composed of two to twenty matrilocal adult females and their immature offspring. Female elephants form strong social ties with members of their natal core group. However, over the course of days or weeks, core groups can divide into units as small as a single adult female and her offspring, or partial and whole core groups might fuse to form a group with other core groups. Pairs or trios of core groups that fuse most often are called 'bond groups' (e.g. the cluster inside the dashed circle in Fig. 2a; Moss & Poole 1983; Wittemyer *et al.* 2005). Whole core groups and bond groups that share similar home ranges are known as clans. In contrast to females, Male elephants disperse from their natal core group at maturity, and never join a new core group permanently. Instead, they roam inside and outside their natal population, searching for mates and forming wide ranging social bonds with other males (Fig. 2b). Bonds between males are predictable but weak (Chiyo *et al.* 2011a; Lee *et al.* 2011). Indeed, males rarely spend more than 10% of their time with any other male (Fig. 2b).

Despite the fluid nature of elephant societies, elephants are able to maintain close ties with kin, especially in populations not heavily impacted by poaching. The elephants in Amboseli National Park, Kenya, have been shielded from heavy poaching since the early 1970s (Moss 2001). In Amboseli, kinship is a strong predictor of female social relationships (Archie *et al.* 2006;

Table 1). In support, while members of the same core group spent variable amounts of time together, average genetic relatedness between females that spent 90% or more of their time in the same group was 0.42 (SE ± 0.05), revealing that these females were almost exclusively mothers and offspring and maternal half siblings (Archie *et al.* 2006; Table 1). Maternal kinship also predicted higher levels of social organization in Amboseli, suggesting that the hierarchical fission and fusion of elephant groups occurs as a process of matrilineal fissioning (Archie *et al.* 2006). In support, 89% of bond groups shared the same mtDNA haplotype— more groups than expected by random chance—and the oldest females in each core group that comprised a bond group were close genetic relatives. Beyond bond groups, mtDNA haplotypes predicted the likelihood that core groups from across the population would fuse to form a group (Archie *et al.* 2006). The mechanism that maintains these ties among distant maternal kin is unknown, but it is possible that elephant calves learn which groups are familiar associates and maintain those ties when they become adults. In addition, social groups that were once part of the same core group might continue to maintain similar home ranges, and so they might have more opportunities to interact and form a group.

Kinship also appears to influence the strength of social relationships between adult male elephants (Chiyo *et al.* 2011a). In Amboseli, males form close bonds with a few animals, and weaker associations with several others, to comprise a network of associates can include tens of other males (Lee *et al.* 2011; Chiyo *et al.* 2011a; Fig. 2b). Among these males, the correlation

between relatedness and association was 0.08 ($P < 0.01$), indicating that kinship predicts a small but significant fraction of the variation in the strength of social relationships among males (Chiyo *et al.* 2011a). It is unknown whether kin-based associations between male elephants occur between maternal kin, paternal kin, or both, but maternal kin should be familiar to each other because they were born into the same core group. The benefits of kin-based associations between male elephants are not known, however, male kin might represent familiar associates for foraging or sparring (Chiyo *et al.* 2011a).

If elephants are like many other social mammals, we might expect relationships between kin to be stronger and more beneficial than those among non-kin (e.g. Rossiter *et al.* 2002; Silk *et al.* 2006; Perry *et al.* 2008). For female elephants, the proposed benefits of sociality are numerous, and relatives and older animals are especially valued social partners (Dublin 1983; Lee 1987; Moss 1988; McComb *et al.* 2000, 2001; Foley 2002). For instance, related females cooperate to care for offspring or and are more likely to form cooperative coalitions (Lee 1987; Archie *et al.* 2011). Older females cooperate to defend young animals against predators by forming a tight defensive ring around young animals (Dublin 1983). Finally, older animals provide important social links between younger members of a matriline and are thought to serve as repositories of social and ecological knowledge (McComb *et al.* 2000, 2001; Foley 2002).

However, poaching removes older animals from elephant populations and disrupts the kin-based association patterns in elephant societies (Poole 1989a; Gobush *et al.* 2009; Wittemyer *et al.* 2009). Table 1 compares the kin structure of elephant populations that have experienced a range of poaching intensities. This comparison reveals several important patterns. First, populations that have experienced heavy poaching tend to have more social groups that contain a greater diversity of mtDNA haplotypes. For instance, 95% of core groups in Amboseli had uniformity of mtDNA haplotypes, as compared to 91% in Samburu National Reserve, Kenya, or 67% in Queen Elizabeth National Park, Uganda (Nyakaana *et al.* 2001; Wittemyer *et al.* 2009; Table 1). Similarly, a greater fraction of bond groups in Amboseli had uniformity of mtDNA as compared to more heavily poached populations (Charif *et al.* 2005; Gobush *et al.* 2009; Wittemyer *et al.* 2009; Table 1). This loss of uniformity of mtDNA haplotypes within core and bond groups probably occurs when female's that have lost their core group to poaching join new core groups with unrelated females. Similar effects can be observed on the percent of core groups where the average pairwise genetic relatedness among core group members is significantly greater than zero. For instance, in Mikumi

National Park, Tanzania only 54% of core groups had pairwise genetic relatedness among group members that was significantly greater than zero, while 80% of core groups had average relatedness significantly greater than zero in both Amboseli and Samburu. This similarity between Amboseli and Samburu is interesting in light of the fact that Samburu has experienced more poaching than Amboseli. However, this discrepancy could be explained by the fact that these populations use different criteria to define core social groups; Amboseli defines core groups based on 40 years of monitoring, while Samburu study uses cluster analysis to define statistically significant groups (Wittemyer *et al.* 2005). Consequently, compared to Samburu, Amboseli core groups contain more animals, and those animals are less cohesive (average association indices among core group members are 0.60 in Amboseli versus 0.84 in Samburu). However despite these differences, genetic relatedness between elephants for a given bond strength was considerably lower in Mikumi and Samburu than in Amboseli, and the correlation between pairwise relatedness and association indices for female elephants is weaker in Samburu and Mikumu than in Amboseli (Gobush *et al.* 2009; Wittemyer *et al.* 2009; Table 1).

Because poaching tends to remove older animals and kin, it might reduce the adaptive value of elephant social relationships (e.g. Moss 1988; Poole 1989a; Gobush *et al.* 2008). Currently, support for this hypothesis is complex; on the one hand, elephants often respond flexibly to a lack of close relatives by forming new social bonds with non-relatives. This pattern is clear from the results in Table 1, which show that females sometimes form new core groups with other females that are not maternal kin. Even in Amboseli, female elephants sometimes lose all of their close maternal relatives due to natural causes or poaching. For instance, five of forty focal females in Amboseli lacked close maternal kin and did not seem to suffer major negative behavioural consequences (Archie 2005; Archie *et al.* 2011). These females were just as likely to be in close physical proximity to other females, had just as many affiliative interactions with other females, and were just as likely to be involved in a cooperative coalition than females without close female relatives (Archie 2005; Archie *et al.* 2011). Other research also demonstrates elephants' social flexibility. For instance, Pinter-Wollman *et al.* (2009) followed the social integration of 150 African elephants after they were moved from two small reserves to a large National Park 160 km away. They found that many translocated females were resilient and formed social associations with other females that were unlikely to be close kin. Those that formed social relationships had better body condition than

those who remained alone, and over time the social barriers lessened between translocated and resident elephants (Pinter-Wollman *et al.* 2009). Hence, results from these studies suggest that female social association patterns are likely resilient to the loss of kin.

However, just because elephants are able to form new relationships does not mean they always do, or that these new relationships have the same benefits as those among close kin. Indeed, while research in Amboseli has focused on the behavioural consequences of losing close kin, research in Mikumi demonstrates both behavioural and fitness-related consequences of poaching. For instance, after heavy poaching in Mikumi, 30% of 102 core groups consisted of single females, indicating that many females failed to form new relationships (Gobush & Wasser 2009). In addition, when females formed new social groups with non-kin, these disrupted groups had fewer beneficial interactions with other social groups. Indeed, disrupted groups had lower average pairwise genetic relatedness, were less discriminating in their relationships with other core groups, and their interactions were more competitive than those of intact core groups (Gobush & Wasser 2009). Moreover, Gobush *et al.* (2008) found that female elephants from disrupted core groups had weaker social bonds, higher glucocorticoid (stress hormone) levels, lower average pairwise genetic relatedness, and significantly lower reproductive output than females from intact groups.

Poaching clearly disrupts elephant societies, and evidence suggests that the removal of kin as social partners has negative consequences, at least for some elephants. However, poaching has multiple effects on the structure of elephant populations, and as yet it is unclear whether the loss of kin itself, or other consequences of poaching—e.g. the loss of older animals, the loss of familiar social partners, or changes in group size—might be more important in determining the functionality of elephant societies. Because poaching removes familiar social partners, females might experience costs because they are forced to form new relationships with strangers, whether they are kin or not. Moreover, there is strong evidence that the loss of older animals could be more important than the disruption of kin structure. Matriarch age predicts female reproductive success (McComb *et al.* 2001), and in Mikumi, core groups that lacked an old matriarch ranged in areas with historically high poaching and had low average pairwise genetic relatedness had higher levels of stress hormones (Gobush *et al.* 2008). One way to gain insight into the relative contributions of kinship, age, and familiarity to the benefits of social relationships for elephants is through longitudinal studies on the effects of the loss of kin or older matriarchs over the course of a

female's life. For instance, if particular kin categories are most important (e.g. mothers and daughters), then we expect the loss of a mother or daughter to alter aspects of female social integration or reproductive success. Similarly, the loss of an old matriarch from a group might create changes in social relationships with altered female fitness after her death. However, if females are effectively able to replace close kin relationships or old matriarchs with other relationships, then it is more difficult to attribute the negative effects of poaching to the loss of kin or matriarchs. Regardless of the cause, poaching clearly has negative consequences for the function of elephant societies, and elephants clearly demonstrate the negative consequences of human actions for on animal social relationships.

Male reproductive success, inbreeding avoidance and the effects of poaching

Breeding behaviour has a large effect on the structure of genetic diversity in animal populations. For instance, in many group-living mammals, a few dominant males sire the majority of offspring in the same social group; hence, over time, genetic relatedness within social groups and genetic differentiation between groups increases (Sugg *et al.* 1996). In such societies, individuals can minimize the risk of inbreeding through sex-biased dispersal (Pusey 1987; Pusey & Wolf 1996; Sugg *et al.* 1996). In elephants, however, males never permanently join a new social group. Instead they search widely for mates, siring offspring in several groups across the population. Females rarely sire offspring with the same male twice, and paternal siblings occur in similar-aged cohorts across the population (Archie *et al.* 2008). Elephants have probably evolved this system because, from a male's perspective, sexually receptive female elephants are a scarce resource. Female elephants gestate their calves for 22 months and nurse those calves for two or three years; hence female elephants are only sexually receptive for a few days every 3–6 years (Moss 1983; Poole & Moss 1989). These breeding patterns have two important consequences. First, because males search widely for mates, they compete for reproductive opportunities with all other males in the population, creating intense male–male competition. Second, because males can sire offspring in any group, they have the opportunity to return and breed in their natal group, or with paternal siblings across the population; this situation increases the risk of inbreeding. Here, we review how sexual selection and inbreeding avoidance shape patterns of reproductive success in male elephants (Archie *et al.* 2007; Hollister-Smith *et al.* 2007; Rasmussen *et al.* 2008). We then discuss the effects of poaching on male reproductive skew and the

maintenance of genetic diversity (Ishengoma *et al.* 2008; Rasmussen *et al.* 2008).

In elephants, intense male–male competition has led to several behavioural, morphological and physiological traits that influence male dominance (Poole 1989b,c; Poole & Moss 1989; Poole *et al.* 2011). Specifically, unlike many male mammals, male elephants grow for their entire adult lives and have extreme sexual size dimorphism such that the largest, oldest males are more than twice the mass of a typical adult female (Roth 1984; Lindeque & van Jaarsveld 1993; Lee & Moss 1995). There are also large size differences between males of different ages. For instance, a 40-year old male might be twice the mass and 30% taller than a 20-year old male (Poole *et al.* 2011). These differences create a dominance hierarchy based on age and size where older, larger males outrank and younger, smaller males (Poole 1989b). In addition, adult male elephants show musth, a physiological state where males have elevated testosterone, aggression, and sexual activity (Poole & Moss 1981; Moss 1983; Hall-Martin 1987; Poole 1987). Males begin to enter musth at around 20 years of age, and maintaining musth for long periods is probably costly; hence, the duration of musth increases as males age such that the youngest males are in only musth for a few days each year, while older males might remain in musth for 2 or 3 months each year (Poole *et al.* 2011). Critical to male reproductive success, musth influences male dominance rank such that, regardless of size or age, males in musth outrank all males not in musth (Poole 1989b).

Genetic paternity analyses demonstrate that, in elephants, age and musth predict reproductive success (Hollister-Smith *et al.* 2007; Rasmussen *et al.* 2008). For instance, in Amboseli, researchers used microsatellite genotypes at eight loci to assign paternity to 119 calves (Table 2). These 119 calves were sired by 36 males that ranged in age from 26 to 59 years old. Among sires, age and musth status strongly predicted reproductive success; 74% of calves were sired by males in musth, and males reached their peak reproductive success between the ages of 45 and 53 (Hollister-Smith *et al.* 2007). In other elephant populations, age and musth status are also strong predictors of reproductive success. For instance, in Samburu most offspring were sired by males in musth, and in both Samburu and Tarangire, the oldest males sired the most offspring (Ishengoma *et al.* 2008; Rasmussen *et al.* 2008; Table 2). Hence, male elephants wait in an age-based queue to mate, and male reproductive success increases with age. This pattern differs markedly from many other social mammals, where males tend to reach peak reproductive success soon after they reach sexual maturity and adult body size (e.g. Clutton-Brock 1988; Le Boeuf & Reiter 1988; Alberts *et al.* 2006). Hence, male elephants appear to represent an extreme among mammals in the extent to which they breed successfully late in life (Hollister-Smith *et al.* 2007).

This intense male–male competition for mates might also influence the evolution of inbreeding avoidance. In particular, if reproductive opportunities are rare, the opportunity costs of inbreeding avoidance might outweigh the benefits of reproduction, even with high costs of inbreeding depression. This problem is important in elephants because males sire offspring in several social groups, and thus males have the opportunity to breed with maternal kin in their natal group and close paternal kin—either daughters or paternal siblings—in other social groups. However, genetic studies reveal that, despite the opportunity to breed with relatives, elephants are largely successful at avoiding inbreeding (Archie *et al.* 2007). In support, an analysis of behavioural and demographic data spanning 28 years of research in Amboseli, found that elephants avoid siring offspring with their close kin (Archie *et al.* 2007). Moreover, male elephants were significantly less likely to

Table 2 Effects of poaching on patterns of paternity in three African elephant populations

Population	Percent population decline due to poaching	Number of calves where paternity was assigned* (and number of calves genotyped)	Number of fathers assigned to calves	Average age (±SD) of the three most successful males	Percent of genotyped calves sired by the three most successful males	Percent of genotyped calves sired by males in musth	Sources
Amboseli National Park, Kenya	30%	119 (279)	36	51 (±2)	13% (36 of 279)	74%	Hollister-Smith *et al.* (2007)
Samburu National Reserve, Kenya	85%	36 (79)	15	40 (±5)	19% (15 of 79)	75% to 80%	Rasmussen *et al.* (2008)
Tarangire National Park, Tanzania	~85%	8 (26)	5	39 (±3)	23% (6 of 26)	–	Ishengoma *et al.* (2008)

* Paternity in Amboseli was assigned at 95% confidence, while paternity in Samburu and Tarangire was assigned at 80% confidence.

engage in sexual behaviours and sire offspring with close kin. Interestingly, these results extended to both maternal and paternal relatives, despite the fact that paternal kin are probably much harder to recognize using behavioural cues alone. It is unknown how elephants avoid their relatives; elephants might simply avoid breeding with natal group members, and thereby avoid maternal kin, but elephants might use unknown behavioural or olfactory cues to recognize paternal kin.

Because age and musth status predict reproductive success among male elephants, and because poaching selectively removes older males from populations, poaching could alter patterns of paternity in elephant populations. For instance, poaching may increase reproductive opportunities for young males. In support, when older male elephants are removed from elephant populations, young males increase the frequency and duration of their musth periods (Slotow *et al.* 2000). Furthermore, this effect disappears when older males are reintroduced into the population (Slotow *et al.* 2000). Genetic analyses confirm that poaching reduces the age of peak reproduction for males. Table 2 compares patterns of paternity in three populations that have experienced a range of poaching intensities. This comparison reveals that reproductively dominant males are younger in poached populations; the average age of the three most successful males was around 40 years of age in Samburu and Tarangire, two populations that experienced greater population declines due to poaching than Amboseli. These males are, on average, around ten years younger than similarly successful males in Amboseli (Hollister-Smith *et al.* 2007; Ishengoma *et al.* 2008; Rasmussen *et al.* 2008; Table 2).

This result—that poaching reduces the age of peak reproduction—suggests that poaching might increase reproductive opportunities for younger males, and hence decrease reproductive skew among males (Rasmussen *et al.* 2008). However, paternity analyses in poached populations do not support this hypothesis. Instead, the results in Table 2 suggest that poaching increases male reproductive skew (Table 2). For instance, in Amboseli, the three most successful males sired 13% of all genotyped calves, while in Samburu and Tarangire, the three most successful males sired 19 and 23% of genotyped calves respectively (Ishengoma *et al.* 2008; Rasmussen *et al.* 2008; Table 2). Similarly, in Addo National Park, South Africa, a population that was founded in 1931 from 11 elephants in 1931, a single male sired around 28% of offspring born over a 15-year period (Whitehouse & Harley 2002). Poaching probably increases male reproductive skew for two reasons. First, poaching rarely removes all of the oldest males in a population; hence the few older males who remain dominate reproduction in the absence of same-aged

competitors (Ishengoma *et al.* 2008). Second, poaching might increase reproductive skew among male elephants by increasing the reproductive tenure of young males (Ishengoma *et al.* 2008). If male elephants begin to breed at a relatively young age in poached populations, those males will lead longer more productive reproductive lives than comparable males in an intact population. Both of these phenomena will tend to increase male reproductive skew.

If poaching increases male reproductive skew, this will have important consequences for the maintenance of genetic diversity in wild elephant populations. Specifically, reducing the number of breeding males will decrease the effective population size of elephant populations and increase the rate at which genetic diversity is lost. Similarly, if the same few males sire the majority of offspring, the risk that individuals will encounter and breed with close kin might increase. This effect could be exacerbated by habitat fragmentation. Elephant populations are increasingly constrained to live in smaller, more isolated patches of habitat. This situation could reduce effective population sizes and increase the loss of genetic diversity from elephant populations. In the future, genetic approaches such as assignment tests will be increasingly important to identify migrants between populations, which may be critical to maintain genetic diversity in isolated populations. In addition, while elephants' abilities to recognize kin and avoid inbreeding might mitigate the loss of genetic diversity, this is not necessarily true. Because we do not really understand how elephants recognize and avoid breeding with relatives, and because human activities might disrupt some social cues that elephants use to recognize kin (e.g. disturbing the structure of female core groups), it is unclear whether inbreeding avoidance will have a large impact on the loss of genetic diversity from elephant populations. Regardless, there is strong evidence that poaching disrupts elephant breeding behaviour, with important consequences for the long-term maintenance of genetic diversity in elephant populations.

Genetic tools in elephant management

While genetic tools have helped to reveal patterns of social relationships and reproduction in elephants, genetic methods have also contributed key information to managers and conservation biologists about elephant population size and forensics. As such, elephants provide a valuable case study for the use of genetic tools to conserve other social species. In this section, we review the utility and success of molecular-genetic techniques to address three conservation issues: to monitor populations of elusive forest dwelling elephants, to

understand the behavioural ecology of crop raiders, and to track sources of illegal ivory in the market.

Genetic methods are common in elephant conservation for two reasons. First, the availability of several, highly polymorphic microsatellite loci in elephants makes it possible to produce multi-locus genotypes that are unique to each individual with relatively few loci (Nyakaana & Arctander 1998; Comstock *et al.* 2000; Archie *et al.* 2003; Nyakaana *et al.* 2005; Table 1 in Okello *et al.* 2005). These unique genotypes are used as individual identification tags in ecological and behavioural studies. Second, genetic tools are unusually common in elephant conservation because of the abundance and success of non-invasive genetic methods and non-invasive sources of DNA in elephants (e.g. fecal-derived DNA). However, even in elephants, DNA obtained from non-invasive sources can be low quality or degraded. Hence, noninvasive genotyping is prone to errors due to allelic dropout, spurious alleles, and null alleles (Jones *et al.* 1998; Holm *et al.* 2001; Shinde *et al.* 2003; Buchan *et al.* 2005). Identifying or controlling for these errors is important because they can alter the conclusions of genetic methods to identify crop raiders, assign parents or source ivory and the resulting management implications. Readers should see several excellent reviews that describe a number of approaches to identify errors in noninvasive genotyping (Waits & Leberg 2000; Waits & Paetkau 2005; Beja-Pereira *et al.* 2009; Morin *et al.* 2010).

Despite the challenges of working with noninvasive DNA, molecular methods have been important in several areas of elephant conservation; for instance, to count the number of individuals in a population, or to assess the impacts of poaching, habitat loss or conservation interventions. This is especially important when species are difficult to count using conventional observation methods such as aerial counting or individual recognition (White *et al.* 1989; Aleper & Moe 2006; Parker *et al.* 2011). This is a particular problem for elephants, because observing elephants while on foot can be risky, and the most direct observations are usually conducted while the observer is in the car, air or a protected platform. Moreover, elephants in forest or woodland habitats are difficult to detect from the air, and consequently aerial counts underestimate infant and juvenile elephants because their visibility is easily obscured by thick vegetation or other elephants. In these situations, elephant population estimates are most often estimated from either dung counts or molecular-genetic census techniques (Barnes 2001; Eggert *et al.* 2003). More recently, some researchers have also used camera traps to count elusive Asian elephants (e.g. Goswami *et al.* 2007). Elephant population estimation from dung census, involves counting the number of dung piles in a given area and converting this to the number of elephants by determining the number of dung piles attributable to one elephant. However, the number of dung piles per elephant is a result of dung accumulation in the environment through elephant defecation and dung removal through dung decay, and this method requires that elephant defecation rates and dung decay rates are known for any given elephant population and locality (Barnes *et al.* 1997).

Often more reliable, molecular census techniques require fresh fecal material for genotyping. Unique genotypes are generated and the sampling history of unique genotypes is used to determine the total animal population using capture-recapture population models (Lukacs & Burnham 2005; Guschanski *et al.* 2009). Although molecular censuses can seem expensive, they might be less costly than aerial counts (Solberg *et al.* 2006). Moreover, the major advantage of the molecular censuses is that they can provide more accurate and precise estimates of population size compared to dung censuses. This is because the precision of a population estimate from dung counts is influenced not only by variance in dung counts, but also by variance in defecation and dung decay rates. In support, a study using molecular capture–recapture sampling techniques in Kakum National Park in Ghana, to estimate the population size of elephants produced more precise population estimate compared to the estimate from the dung counts (Eggert *et al.* 2003). Another advantage of molecular census techniques is that, unlike dung counts, genetic information can provide information on sex ratios, effective population sizes and demographic history (Eggert *et al.* 2003; Okello *et al.* 2008). Indeed, molecular markers for sex identification have been developed for a number of species including elephants. The sex identification locus in elephants has been used successfully in estimating sex ratios of elephant populations using non-invasive DNA sources (Eggert *et al.* 2003).

The second area where genetic tools have contributed to elephant conservation is in helping to solve human–wildlife conflict. Human–wildlife conflict can accelerate local extinction of already declining populations. For instance, some carnivore and elephant populations have been nearly extirpated as a result of conflict with humans (Haigh *et al.* 1979; Tumenta *et al.* 2009). In elephants, the most common cause of conflict with humans is crop raiding. Wildlife agencies and local farmers often retaliate by killing suspected raiders, and such killing can represent a major cause of elephant mortality (Mpanduji *et al.* 2004; Obanda *et al.* 2008). Although crop raiding is an old and common problem for elephants, little is known about the behavioural ecology of populations involved in crop raiding. This

lack of knowledge is important because the prevailing paradigm for managing problem animals has been targeted removal of offending individuals (Linnell *et al.* 1999). The assumption is that these few individuals are causing most or all of the conflict and their elimination should mitigate conflict. To manage human elephant conflict, there is need to identify the patterns of raiding by individual animals in order to determine whether there are problem individuals and establish the characteristics of these individuals. If only certain individuals are raiding, they might be the target of management strategies. On the other hand, if this assumption is wrong, then the management strategies might not work. Testing this assumption has proved difficult because most raiding happens at night, and it is difficult to locate and identify raiders during the day. However, the availability of feces from raiders in raided farms make non-invasive genetic census tools a more feasible and reliable method for studies of these elusive behaviours.

In support, non-invasive molecular-genetic techniques have proved useful in understanding the behavioural ecology of populations that raid crops. For example, a genetic study in the Amboseli ecosystem, southern Kenya confirmed that a few individuals caused most of the raiding, but revealed even a more complex pattern of raiding by elephants (Chiyo *et al.* 2011b). Specifically, while 10 males were responsible for 56% of the raiding events by elephants, an additional 74 elephants were occasional raiders and were responsible for the remaining 44% of raids (Chiyo *et al.* 2011b). In this study, genetic methods proved more reliable in estimating the total number of raiders and were less biased than observational methods, which tended to only detect raiders from populations habituated to tourism. However, the major disadvantage of using molecular tools to identify and determine patterns of crop raiding is that the genetic identifications have to be matched with physical or photo identifications. Such physical identities are often difficult to collect and involve long-term monitoring of elephant populations. However, despite this caveat, molecular methods are still the most powerful tools for detecting patterns of raiding by individuals across populations. These studies will generate consensus behaviour patterns of populations that come into conflict with humans, providing useful information for managing human–elephant conflict.

Finally, the third area where genetic tools have made major contributions to elephant conservation is in the forensics of poaching. Elephant poaching for ivory represents a serious threat to their conservation and is currently on the rise (Wasser *et al.* 2007, 2010; Douglas-Hamilton 2008; Dunham 2008). Elephants are considered threatened, and ivory sales are therefore regulated by the Convention on International Trade in Endangered Species (CITES). However, the presence of a market for legal ivory also encourages illegal exploitation of elephant populations elsewhere (Wasser *et al.* 2010), creating a need to identify sources of illegal ivory.

Current efforts to contain illegal ivory sales depend on two forensic approaches to determine the source of ivory. The first approach relies on genotyping ivory samples at highly polymorphic loci, and then using assignment tests to pinpoint specific geographical origins of illicit ivory (Wasser *et al.* 2004, 2007). The second approach uses X-ray or stable isotope techniques to analyze the elemental composition of ivory (van der Merwe *et al.* 1990; Koch & Behrensmeyer 1992; Takeuchi *et al.* 1996, 1998; Kautenburger *et al.* 2004). X-ray methods quantify trace amounts of several elements in ivory, which vary regionally or even locally depending on the minerals in the soils. Similarly, stable isotope ratios, particularly carbon, nitrogen and strontium isotopes in collagen extracted from ivory reflect differences in vegetation, rainfall as well as geology. For example the carbon isotope ratio ($^{13}C/^{12}C$) or $\delta^{13}C$ is lower when C_3 plants such as most herbs, shrubs and trees dominate the elephant diet and is higher when C_4 plants or grasses dominate their diet. $\delta^{13}C$ is therefore used to distinguish ivory from elephants inhabiting forests/woodland or grassland habitats.

All of these approaches, whether genetic or isotopic, require reference measures for elephant populations from different locations across the continent. There is currently more reference information for molecular methods than isotope-based methods; for instance, there are currently isotope reference values (carbon, nitrogen and strontium) for 23 elephant populations from 10 countries, while genetic sampling includes 399 reference genotypes from 7 to 16 polymorphic microsatellite loci, collected from 28 locations in 14 countries across the African continent (i.e. 85% of the elephants range) (van der Merwe *et al.* 1990; Wasser *et al.* 2004). Genetic methods have an additional advantage in that genotype frequencies are correlated in space; hence, researchers can use spatial smoothing procedures to infer the source of ivory from locations where there are no reference genotypes (Wasser *et al.* 2004). Although the elemental analysis of ivory using isotope analysis or X-ray analysis of trace metals in ivory can produce distinctive signatures for local elephant populations, this method may fail to precisely assign ivory from areas that are distant but with similar climate and geology because they will have a similar stable isotope signature in their ivory.

The results of these studies indicate that molecular tools are often more accurate than non-genetic approaches for understanding elephant conservation

issues. However, molecular genetic tools continue to be expensive, and the future utility of molecular techniques in elephant conservation will depend on the availability of cheaper and reliable alternative methods. However, despite these costs, molecular tools are more accurate than dung counts in estimating population size, provide more details about the identities of crop-raiders than observational approaches, and provide the most accurate forensic information about the sources of ivory (Eggert *et al.* 2003; Wasser *et al.* 2004, 2007; Chiyo *et al.* 2011b). While biologists will need to weigh the value of genetic data against the availability and expense of other methods, genetic tools are likely to have a long and useful future in elephant conservation.

Conclusions and future directions

The research reviewed here reveals patterns of elephant behaviour, and the effects of poaching on elephant social relationships and genetic structure (summarized in Fig. 1). Under natural conditions, females form beneficial social relationships with relatives and older, experienced animals. Poaching disrupts these relationships by removing older animals and kin, which can limit the adaptive value of female relationships. We are just beginning to understand the consequences of these effects, but the loss of these key social partners could lead to lower reproductive rates for females. For males, age is an important predictor of reproductive success for male elephants. Poaching appears to reduce the age of first reproduction for males and lead to increased reproductive skew, which may increase the rate at which genetic diversity is lost from natural elephant populations. In addition to the effects of poaching on behaviour, genetic tools are also often useful for providing basic information for population managers and policy makers. Genetic approaches provide unprecedented detail for censusing elusive populations, understanding nocturnal crop-raiding behaviour and tracking the sources of ivory in the market. The advent of new, high-throughput, genomic-level tools for elephant populations will likely improve these techniques even further. For instance, genomic resources for African elephants should aid researchers in the development of thousands of single nucleotide polymorphisms (SNPs), which could greatly increase our power to identify individuals from noninvasive DNA or track sources of ivory. Similarly, genomic information will help improve our understanding of functional genetics in elephants; for instance to identify genes involved in resistance to novel pathogens. The relatively long history of genetic methods to understand elephants indicates future potential for elephant evolutionary and conservation genetics.

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