



## Orphaning and natal group dispersal are associated with social costs in female elephants

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Social environments are fundamental to fitness in many species. In disrupted societies, the loss of important partners may alter social environments for surviving individuals. African elephants, *Loxodonta africana*, have experienced age-selective mortality linked to the ivory trade, and the resulting social costs for surviving young elephants are unknown. In this study, we followed orphaned female elephants and nonorphaned counterparts in Kenya's Samburu and Buffalo Springs National Reserves to elucidate whether orphaning and related dispersal behaviour incur social costs. There were clear social differences between orphans and nonorphans, most notably in that orphans tended to receive more aggression than nonorphans. Dispersal from natal groups was a behaviour found exclusively among orphans. Differences in social environments of orphans that remained in their natal groups and those that dispersed were also found in the form of dispersed orphans receiving more aggression while feeding than those that remained in their natal group. Our results suggest that orphaning in elephants is associated with social costs, and that these costs are amplified for orphans that disperse from their natal groups. Future research should identify the relationship between the social costs of being an orphan and fitness, which may be important to the recovery of populations affected by the ivory trade and other forms of disruption.

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Early social environments may affect fitness in long-lived species (McDonald, 2007; Ruploh, Bischof, & von Engelhardt, 2014; Stanton & Mann, 2012), and the absence of social partners in particular during early life may reduce fitness. In moose, *Alces alces*, for example, maternal presence is associated with higher juvenile overwinter survival (Berger, 2012). Social connectivity is predictive of survival in savannah baboons, *Papio cynocephalus* (Archie et al., 2014) and killer whales, *Orcinus orca* (Ellis et al., 2017), and of status that is associated with reproductive opportunity in long-tailed manakins, *Chiroxiphia linearis* (McDonald, 2007). The ability of young animals to buffer the effects of social loss can be important for survival into adulthood and reproduction (Engh et al., 2006; Nunez, Adelman, & Rubenstein, 2015). Social structure that facilitates access to alternative partners, like fission–fusion dynamics in which social group size and composition vary, can be particularly beneficial to retain important social relationships (Bednarik, Fehl, &

Semmann, 2014; Farine et al., 2015) by allowing animals to adjust their interactions to changing scenarios (Aureli et al., 2008). However, the costs associated with social adjustments in such systems and the costs of social loss generally have received little attention.

While relatedness and bond strength are highly correlated for many social animals (Silk, 2007), cooperative bonds among non-relatives indicate a range of social strategies beyond those based on kin (Cameron, Setsaas, & Linklater, 2009; Clutton-Brock, 2009; Griffin & West, 2002). For example, vampire bats, *Desmodus rotundus*, regurgitate for unrelated roostmates, which is thought to expand their future meal donor networks (Carter & Wilkinson, 2015), and spotted hyaenas, *Crocuta crocuta*, choose social partners based on dominance rank to maximize feeding opportunities (Smith, Memenis, & Holekamp, 2007). While some work has demonstrated that individuals strengthen bonds with other relatives in response to familial loss (Silk, Altmann, & Alberts, 2006), social expansion beyond kin following bond loss has also been found: army ants (*Dorylus molestus*) with a dead queen fuse with neighbouring colonies despite low relatedness (Kronauer, Schöning, D'Etterre, & Boomsma, 2010), and elephants (Charif et al., 2005; Moss & Lee, 2011; Vidya, Varma, Dang, Van Thanh, &

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Sukumar, 2007; Wittemyer et al., 2009) and humans (Goldenberg, 2009) strengthen bonds with nonkin in response to severe societal disruption. Quantifying social interaction differences across individuals with different histories can elucidate relative costs and benefits of social expansion following disruption, offering insight regarding the degree to which such behaviour is compensatory and the nature of associated costs.

African elephant, *Loxodonta africana*, populations have experienced increased ivory poaching over recent years, which typically targets older animals for their larger tusks (Chiyo, Obanda, & Korir, 2015; Wittemyer, Daballen, & Douglas-Hamilton, 2013; Wittemyer et al., 2014). Older females act as repositories of information (McComb, Moss, Durant, Baker, & Sayialel, 2001), affect the calving success of family members (Lee, Fishlock, Webber, & Moss, 2016), and provide access to preferred resources through their dominance status and ecological knowledge (Foley, Pettorelli, & Foley, 2008; Wittemyer, Getz, Vollrath, & Douglas-Hamilton, 2007). Loss of old females therefore can present a challenge for the elephants bonded to them as fitness may be affected by such loss. Previous work has revealed that social restructuring occurs following deaths, leading to network resiliency (Goldenberg, Douglas-Hamilton, & Wittemyer, 2016; Wittemyer et al., 2009). However, the consequences of this process remain unclear.

The social interaction patterns of young elephants provide an opportunity to understand the consequences of social disruption. Elephants are highly tactile and interactive, and conspecific affiliation is an important part of social integration in this species (Poole & Granli, 2011). Aggressive interactions may be associated with physiological (Sapolsky, 2005) and opportunity costs, as aggression is often related to access to critical resources in this system like water points, ephemeral forage and shade (Wittemyer & Getz, 2007). Here, we recorded the affiliative and aggressive behaviour of female orphans and nonorphans to elucidate postdisruption social costs in a population that experienced a prolonged period of high mortality associated with ivory poaching (Goldenberg et al., 2016), testing the following predictions: (1) maternal loss is related to social costs in female elephants, manifested as orphans receiving more aggression and experiencing less affiliation than nonorphans; (2) orphans will be more likely to disperse from their natal groups than nonorphans; and (3) social costs in the form of more aggression and less affiliation will increase to orphans dispersing from their natal groups. We discuss the implications of our results for understanding social integration and their relevance to threatened populations.

## METHODS

### Data Collection

We collected data on the individually identified savannah elephants (*L. africana*) inhabiting the Samburu and Buffalo Springs National Reserves in northern Kenya (0.3–0.8°N, 37–38°E) between May 2012 and September 2017 (Wittemyer, 2001). The elephants that use these unfenced reserves number approximately 1000, and are a part of the larger Laikipia-Samburu population (Litoroh, Ihwagi, Mayienda, Bernard, & Douglas-Hamilton, 2010). Established transects were traversed near daily across all seasons, during which we recorded the activity, identities of all elephants encountered and observation accuracy following established protocol. Female savannah elephants exhibit a high degree of fission–fusion sociality with families joining together and separating regularly, although family groups themselves are highly cohesive (Douglas-Hamilton, 1972; Moss, 1988). Female elephants can be found in aggregations composed of cow/calf groups or mixed sex groups, which tend to be larger during the wet season

when resources are more abundant (Wittemyer, Douglas-Hamilton, & Getz, 2005). We considered individuals to be together when in an aggregation that was behaviourally coordinated and spatially cohesive within 500 m of an observer-estimated centre consistent with previous work in this population (Wittemyer et al., 2005). Ages were known from birth records or estimated for elephants over 20 years of age to an accuracy of approximately 5 years (Moss, 1996; Rasmussen, Wittemyer, & Douglas-Hamilton, 2005). Elephants were assigned as dead when their carcasses were found or when absent from their core social groups on more than three consecutive sightings (Wittemyer et al., 2013). This population experienced high mortality in older age cohorts beginning in 2009 with a severe drought that was followed by a rise in poaching over several years (Wittemyer et al., 2014). Mortality affected families differently, in essence creating a natural removal experiment in which some families were disrupted while others were not (Wittemyer et al., 2013).

We conducted ad libitum focal sampling (Altmann, 1974) ('follows') on orphan and nonorphan females ranging from 6 to 17 years old that were not mothers. We chose this age range to maximize sample size without including younger elephants that have a lower likelihood of survival (Wittemyer et al., 2013), although a few study animals died over the course of the study ( $N_{\text{orphans}} = 2$ ,  $N_{\text{nonorphans}} = 2$ ). Elephants in this population are weaned at approximately 4 years of age and females reach primiparity at an average age of 11.34 years (Wittemyer et al., 2013). We focused on nonmothers to elucidate social behaviour in a particular life stage apart from parental care. We focused on females because female and male elephants exhibit distinct social behaviour with females remaining in a matriarchal society. We conducted follows separately when animals were feeding and resting because of the higher rates of interaction associated with the latter activity during which animals cluster together under spatially concentrated shade. Animals were only followed in a given activity if others in their group were engaging in the same activity. During follows, we recorded all interactions and whether focal animals initiated or received interactions (Altmann, 1974). Interaction types were defined following previous specifications (Archie, Morrison, Foley, Moss, & Alberts, 2006; Poole & Granli, 2011) (Table 1). Focal follows continued until one of the following occurred: (1) the animal went out of sight, (2) the animal switched activity or (3) the follow reached 30 min. We collected no more than 60 min total on a given animal in a given sampling day (30 min feeding, 30 min resting) to control for behavioural autocorrelation. Because this study involved recording focal behaviour of identified individuals, we could not record data blind.

### Ethical Note

Our research was conducted with permission from the Kenya Wildlife Service, the Samburu and Isiolo governments and Colorado State University, and in compliance with animal welfare guidelines (IACUC 12-3414A). Behavioural observations were conducted on a population of elephants that are habituated to vehicle presence as a result of decades of exposure to tourists and researchers. The observer approached groups of elephants slowly and parked in a location that would not interfere with elephant activity, and took care to remain quiet for the duration of observations. As such, disturbance to these wild animals was minimized.

### Data Analysis

Core groups were assigned by constructing clustering trees from pairwise association index values calculated using aggregated survey data (Ginsberg & Young, 1992). Structural change points on

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