



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, Pettoirelli, & 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

Table 1

Ethogram of elephant interactions recorded during focal sampling (modified from Goldenberg & Wittemyer, 2017)

	Interaction	Description	
Affiliative	Alloparental	A protects/comforts B (a calf that is not her own; associated with calf crying or environmental stimulus)	
	Allosuckling	A attempts to breastfeed from B	
	Body rub	A rubs B with her body	
	Ear brush	A brushes her ear on B	
	Greeting	A rumbles when A and B meet	
	Head rub	A rubs B with head	
	Herd	A rubs B, resulting in their coordinated movement	
	Playful fight	A and B intertwine heads and spar with no escalation	
	Playful head rest	A rests head on B's body	
	Test mouth	A holds trunk to B's mouth	
	Trunk grasp	A grabs B's trunk	
	Trunk touch	A touches B with trunk	
	Tusk rub	A rubs B with tusk	
	Aggressive	Displacement	A approaches B, B leaves
		Forward trunk swing	A swings trunk in direction of B
Kick back		A kicks B with back foot	
Pursuit		A chases B	
Push		A pushes B	
Stand tall		A faces B with head held above shoulders	
Supplant		A approaches B, A takes B's place	
Tusk		A hits/pokes B with tusks	

cluster trees of associations were used to define group cutoff points that represented shifts from closely associated to more loosely associated individuals (described at length elsewhere: Goldenberg et al., 2016; Romesburg, 1984; Wittemyer et al., 2005). Groups were defined using data before and following the period of increased mortality to determine whether animals dispersed from their natal groups. Dispersal was considered to occur if an elephant joined a new core group without other members of her natal group (i.e. exclusive of fission events within her natal group). We ran a logistic regression including orphans and nonorphans to test our prediction that being an orphan was predictive of dispersal ($N = 65$, see [Supplementary Material](#)), treating dispersal as the response variable and excluding animals that could be considered either orphans or nonorphans (i.e. they were orphaned after the study began). We also excluded animals about which we did not have prior grouping data. Because dispersal is a rare event, we extended the sample for this regression to include all weaned-age elephants without calves for which grouping patterns were known regardless of whether they were focal individuals. Orphan status (0 = nonorphan, 1 = orphan) and core group size (represented as the number of adult females) at the start of the study were included as covariates.

To test our predictions regarding the social costs of being orphaned and dispersing, we modelled the total number of affiliative interactions (the sum of initiated and received) and the number of aggressive interactions received during a focal follow using negative binomial regressions that treated individual elephants as random effects nested within core groups (see [Supplementary Material](#)). Negative binomial models were employed to account for overdispersion in counts of interactions during focal follows, with random effects used to account for repeated sampling of the same individuals and the nested structure of having multiple focal individuals from the same core group. We limited aggressive interactions to those received to more directly focus on social costs. We considered low affiliation rates to be a form of social cost given the assumption that affiliation measures the degree to which an animal is socially integrated, and we therefore included the sum of received and initiated affiliative

interactions rather than only a single direction. We excluded interactions between nonorphans and their mothers to isolate the different nonmaternal social environments experienced by focal individuals (Andres, 2013). Because maternal interactions are central to the social environments of nonorphans, however, we consider maternal interactions independent of models. We conducted separate models for feeding and resting follows.

We ran two sets of models: the first set was designed to test our first prediction assessing the impact of being orphaned on interaction rates and included both orphans and nonorphans ('all animals') with a binary covariate indicating whether the focal animal was an orphan (feeding: 39 orphans, 27 nonorphans, 269.96 h of observation; resting: 34 orphans, 20 nonorphans, 51.97 h of observation). The second set was designed to test our third prediction assessing the social costs of orphan dispersal and, therefore, included a subset of the full data set composed of orphans ('orphans only') with a binary covariate indicating whether the orphan dispersed from her natal group (feeding: 173.25 h of observation; resting: 33.5 h of observation). The average number of minutes followed between orphans and nonorphans did not differ (Kruskal–Wallis: $\chi^2_1 = 0.502$, $P = 0.478$; median_{minutes} = 146, IQR_{minutes} = 65–506.75). To account for different activities, which inherently entail different degrees of social contact, we ran eight types of models: feeding affiliation, feeding aggression, resting affiliation and resting aggression for all animals and for orphans only.

Differences in rates of interaction may be attributable to circumstances prior to the disrupted period unrelated to orphaning. We therefore assessed whether core group sizes differed between orphans and nonorphans prior to the period of orphaning and whether orphans and nonorphans were born to mothers of different ages. Orphans and nonorphans did not differ in the sizes of the groups they belonged to prior to the orphaning period (Kruskal–Wallis: $\chi^2_1 = 1.277$, $P = 0.259$). Orphans were born to significantly older mothers than were nonorphans (Kruskal–Wallis: $\chi^2_1 = 4.951$, $P = 0.026$). We therefore included maternal age at the focal animal's birth as a covariate in all global models. Each global model also included control variables expected to influence interaction rates: focal animal age and aggregation size. Additionally, the orphans-only global models included the age at which focal animals were orphaned to account for changes in social integration over time. To isolate the most important variables related to social interaction, we ran subsets of global models including all combinations of control variables ([Supplementary Table S1](#)) and compared models using Akaike's information criterion corrected for small sample sizes (Burnham & Anderson, 2002). We discuss results from the highest ranked models.

We included the log length of the follow as an offset to control for observation time (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Pearson correlations among covariates did not exceed $r = |0.60|$. We standardized continuous predictor variables $\left(\frac{x-\bar{x}}{\sigma}\right)$ prior to running models for ease of convergence and interpretation, and present results significant at the $\alpha = 0.05$ level and those marginally nonsignificant below $\alpha = 0.10$. Analyses were done using the 'glmmTMB' (Magnusson et al., 2017) and 'MuMIn' (Barton, 2018) packages in R v.3.4.2 (R Development Core Team, 2010).

RESULTS

Rates of affiliative and aggressive interactions among focal individuals differed by activity and between orphans and nonorphans (Table 2). In support of our first prediction that maternal loss is related to social costs in female elephants, top models including all animals demonstrated that there were social costs to being an orphan unrelated to conditions prior to orphaning. Specifically,

Table 2
Median (interquartile range) values of individual average interaction rates (interactions/min) in models including all animals

	Feeding		Resting	
	Affiliation	Aggression	Affiliation	Aggression
Orphan	0.09 (0.05–0.15)	0.01 (0–0.02)	0.63 (0.35–1.29)	0.01 (0–0.03)
Nonorphan	0.09 (0.02–0.20)	0 (0–0.01)	0.68 (0.16–1.35)	0 (0–0)

orphans were more likely to receive aggression than nonorphans (feeding: $P = 0.036$; resting: $P = 0.048$; **Figs 1 and 3**). For context, we calculated aggressive interactions of mothers towards their daughters despite not including these interactions in models (see Methods). Such interactions accounted for an average 9.79% of nonorphan feeding interactions and 0% of nonorphan resting interactions for nonorphans with nonzero interaction totals ($N_{\text{feeding}} = 16$, $N_{\text{resting}} = 5$).

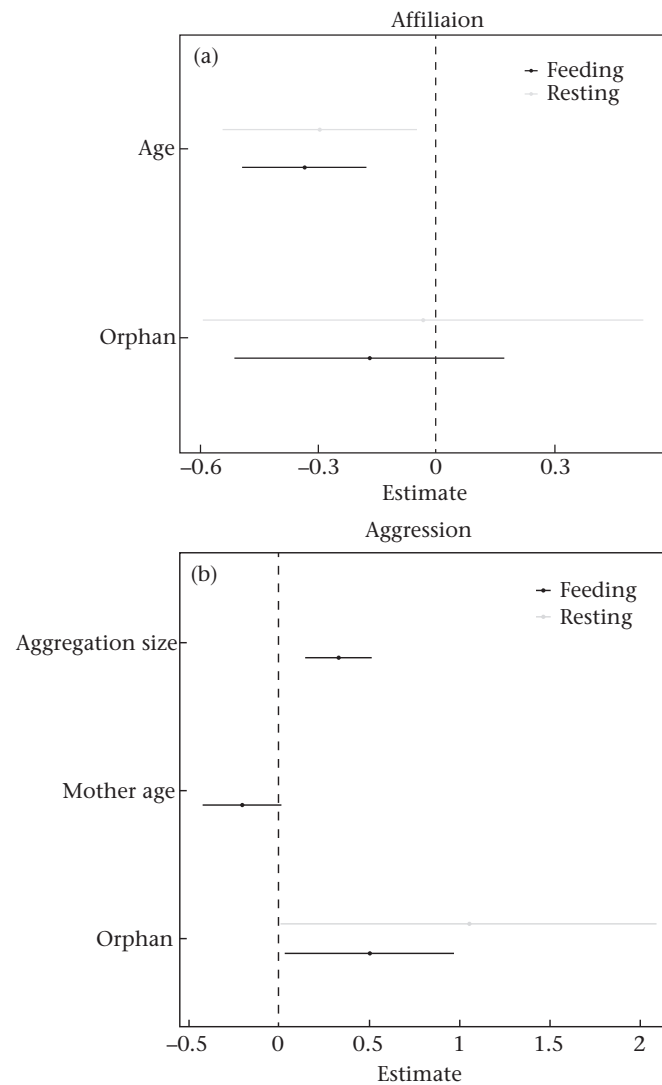


Figure 1. Coefficient estimates for covariates influencing (a) affiliative and (b) aggressive interaction rates when resting and feeding in top models for all animals, which included both orphans and nonorphans. The orphan covariate indicates relative differences between interaction rates of orphans and nonorphans. Covariates that were not retained in top models and thus not depicted added no additional explanatory information. Error bars represent 95% confidence intervals.

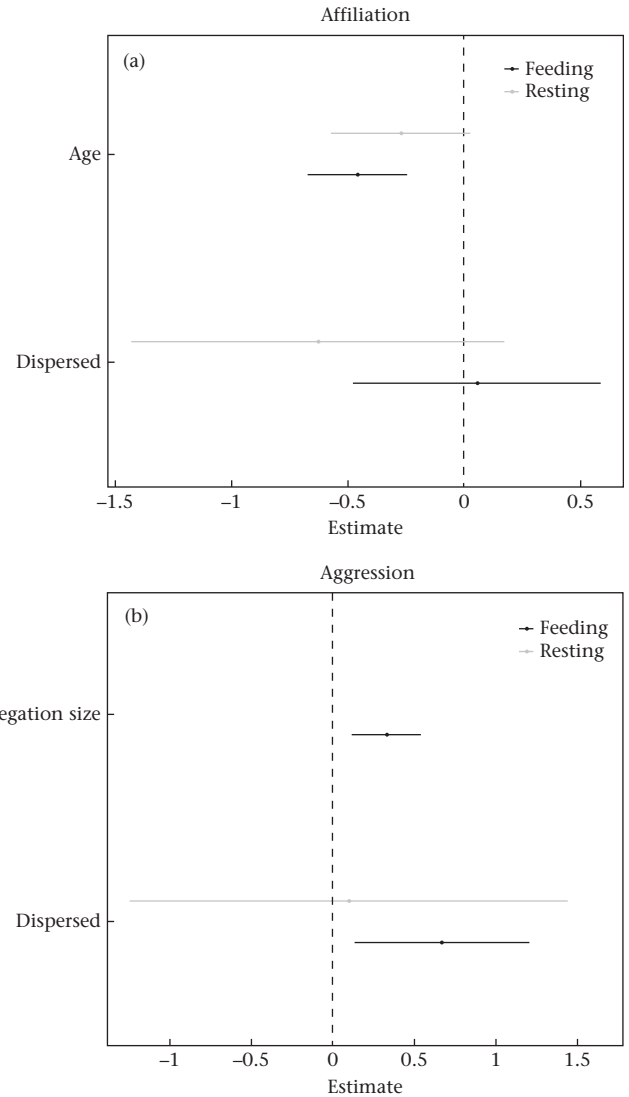


Figure 2. Coefficient estimates of covariates influencing (a) affiliative and (b) aggressive interaction rates when resting and feeding in top models for orphans only. The dispersed covariate indicates relative differences between the interaction rates of orphans that remained with their natal group relative to those that dispersed. Covariates that were not retained in top models and thus not depicted added no additional explanatory information. Error bars represent 95% confidence intervals.

Aggregation size was retained in both top models for feeding aggression and was positively predictive of aggression, with more aggression occurring in larger aggregations (all animals: $P < 0.001$, orphans only: $P = 0.003$). Mother age explained enough variation to be retained in the top model for feeding aggression of all animals. Elephants born to younger mothers tended, although nonsignificantly ($P = 0.072$), to receive more aggression. The ranking of a more complex model in the feeding aggression set for all animals that included the age covariate indicated that focal animal age was an uninformative parameter in this context. Despite comparable AIC_c values (within $\Delta AIC_c = 2$ units per added parameter) (Arnold, 2010) within the feeding aggression model set for orphans only, more complex models that included mother age, age at orphaning and age did not reduce deviance any more than the simpler model including aggregation size and the dispersed covariate. No control variables in the model sets for aggression while resting explained variation enough to be included in top models, despite comparable AIC_c values.

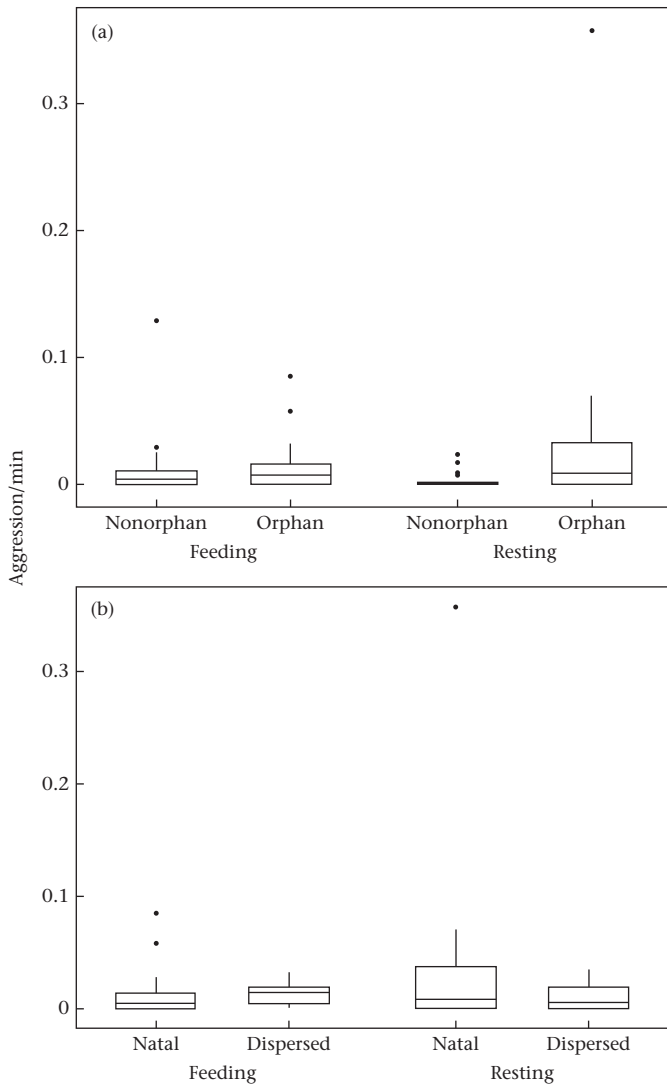


Figure 3. Rates of aggression received by (a) orphans versus nonorphans and (b) natal versus dispersed orphans. Distributions are calculated using the average rate per individual. Horizontal lines represent median values, boxes represent interquartile intervals and vertical lines represent range excluding outliers.

In contrast to our first prediction, we did not find evidence of decreased affiliation for orphans relative to nonorphans. Being an orphan was unrelated to affiliation in either activity in top models (feeding: $P = 0.331$; resting: $P = 0.907$; Fig. 1, Table 2). However, models did not include interactions between nonorphans and their mothers, which accounted for an average 13.17% of feeding affiliative interactions and 23.60% of resting affiliative interactions for nonorphans sampled with nonzero interaction totals ($N_{\text{feeding}} = 22$, $N_{\text{resting}} = 20$). The age control variable was retained in all top models for affiliation, and was significantly negatively related to feeding ($P < 0.001$) and resting ($P = 0.020$) affiliation in top models for all animals and to feeding affiliation ($P < 0.001$) in the top model for orphans only (Figs. 1 and 2). More complex models with comparable AIC_c values included uninformative parameters that did not improve the simpler top models.

In support of our second prediction that orphans would be more likely to disperse from their natal groups than nonorphans, the only elephants that dispersed into new core groups were orphans. However, the orphan covariate in the logistic regression predicting dispersal was not significant (coefficient estimate (SE) = 18.669

(3011.586), $P = 0.995$), likely related to the rarity of dispersal ($N = 7$ of 35 orphans). The number of adult females in an animal's natal group at the start of the study was significantly negatively related to dispersal (coefficient estimate (SE) = -1.425 (0.663), $P = 0.032$), indicating that small families are correlated with dispersal.

Finally, our predictions regarding increased social costs for dispersing orphans were partially supported. Dispersal from a natal group was unrelated to affiliation in the top models for either activity (feeding: $P = 0.837$; resting: $P = 0.127$; Fig. 2, Table 3). However, dispersal was significantly positively related to received aggression while feeding ($P = 0.015$; Fig. 3), although not while resting ($P = 0.886$).

DISCUSSION

There is a rich body of literature on social relationships in animal populations (Silk, 2007), but we lack an understanding of behaviour in social environments that are disrupted (Firth et al., 2017). Maternal loss may be associated with fitness costs for young animals even after they are weaned, which may be related to social processes (Andres et al., 2013; Berger, 2012; Tung, Archie, Altmann, & Alberts, 2016). Previous work in our study system has shown that disruption precipitates dispersal out of natal core groups, presumably to improve altered social context (Goldenberg et al., 2016; Wittemyer et al., 2009). Indeed, the only animals to disperse in our sample were orphans, and our analysis suggests that they do so as a last resort in response to degraded natal groups. Our models showing higher received aggression for orphans shed light on the associated social costs of orphaning and related dispersal, contributing to a larger understanding of sociality in the context of perturbations and providing insight into the response of a threatened species to ongoing disruption.

While controlling for social influences unspecific to orphaning, we found clear social costs of being orphaned in the form of received aggression. Being the recipient of aggression may be costly for a couple of reasons. First, aggressive encounters have been linked to physiological responses in other species, which when frequent, may be associated with higher rates of pathologies (Sapolsky, 2005). If stress increases as more aggression is received, elephant orphans may experience corresponding physical costs. Second, aggressive interactions often relate to resource access in the drought prone semi-arid savannah system where we conducted our study (Wittemyer & Getz, 2007), suggesting that orphans may lose access to vital resources as recipients of conspecific aggression.

Our results did not indicate that orphaning was associated with a decrease in affiliative interactions. While this suggests orphans and nonorphans engage in affiliative interaction with nonmaternal conspecifics at the same relative rate, the influence of excluding maternal interactions in our analyses is notable. Elephant juveniles have high rates of interactions with their mothers, which are key social partners throughout their lives. Therefore, exclusion of this important social partner alters the perception of the overall social interaction rates of nonorphaned individuals. As such, orphans have lower rates of affiliative interactions in general than nonorphans when considering the full interaction environment.

Table 3

Median (interquartile range) values of individual average interaction rates (interactions/min) in models including orphans only

	Feeding		Resting	
	Affiliation	Aggression	Affiliation	Aggression
Natal	0.10 (0.05–0.16)	0.01 (0–0.01)	0.74 (0.42–1.42)	0.01 (0–0.04)
Dispersed	0.09 (0.04–0.11)	0.01 (0–0.02)	0.29 (0.06–0.59)	0.00 (0–0.02)

Dispersal into new groups was observed exclusively for orphans, with nonorphaned individuals staying in their natal groups throughout the study (and longer-term data suggests for life). Dispersal among orphans was correlated with higher rates of received aggression while feeding but not while resting. Resting elephants often cluster with their closest associates, and these results may reflect peripheral positioning by orphans, which was commonly observed for dispersed orphans (Goldenberg & Wittemyer, 2017). Being peripheral to social groups has also been recorded in immigrant spider monkeys, *Ateles geoffroyi* (Ramos-Fernández, Boyer, Aureli, & Vick, 2009), and in reindeer, *Rangifer tarandus*, orphans maintain a greater distance to adults than do nonorphans (Holand et al., 2012). Such peripheral positioning may be a way for orphans to avoid aggression from more dominant animals.

We previously demonstrated that elephants restructure association patterns to resemble their prepoaching networks (Goldenberg et al., 2016); the present finer-scale results indicate that social interactions within this context differ between orphans and nonorphans. In addition to differences in interaction rates, other work has shown orphans to have different social partners, where orphans tended to affiliate with agetates or subordinate group members while nonorphans associated more with adult females (Goldenberg & Wittemyer, 2017). Thus, fine-scale social interactions within restructured networks differ in several ways, indicating that the social turmoil caused by orphaning is more substantial than initial interpretations based on population-level social network analyses.

While we focused on orphans that survived long enough to study, we observed unaffiliated young females over brief periods that subsequently disappeared. The fate of these animals is unknown, but we suspect they did not survive (one such individual that we radiocollared died within a year outside the reserves). Conversely, we have observed animals orphaned over a decade ago that became fully integrated into new groups (G. Wittemyer, personal observation). Our observations therefore indicate a diversity of behavioural outcomes among orphans that may be associated with differential fitness, and that may manifest over longer periods. Our results may merely be capturing a snapshot of a transitional social process that occurs over many years. Continued monitoring of these recent orphans will reveal how social costs change or accumulate with time. Additionally, we note that by focusing on elephants that were frequently sighted within the protected areas, our sample may not capture the full extent of social costs experienced by orphaned elephants.

In addition to the variables of orphan and dispersal status, there were several variables that influenced interaction rates unrelated to our predictions concerning orphaning. Unsurprisingly, age tended to be negatively related to affiliative interactions. Previous work has shown that younger elephants are more interactive (Goldenberg et al., 2016; Lee, 1987), which is thought to facilitate exploration of their social environments as in other species (Patriquin, Leonard, Broders, & Garroway, 2010; Williams & Lusseau, 2006). Similarly, the positive relationship between aggregation size and received aggression among focal animals reflects the social patterns of the species, whereby elephants use opportunities when families temporarily fuse to determine and reinforce dominance relationships (Wittemyer & Getz, 2007; Wittemyer et al., 2005). Although focal animal age was not related to received aggression as expected given the strong correlation between age and dominance in this species (Archie et al., 2006; Wittemyer & Getz, 2007), there was a nonsignificant tendency for calves born to younger mothers to receive more aggression than calves born to older mothers. Thus, mothers may influence the social environments of their daughters in a number of ways.

Demographic parameters are often the focus of studies on overexploited populations (Bragina et al., 2015; Servanty et al., 2011), but indirect effects like altered social environments should be considered in population monitoring of species dependent on social processes (Milner, Nilsen, & Andreassen, 2007). The downstream demographic effects of orphaning linked to social environments likely play an important role in the recovery of elephant populations. Linking social environments experienced by orphans to long-term survival, fecundity and physical condition will provide richer insight into the response of elephant populations to poaching.

Conflict of Interest

We declare no conflicts of interest.

Acknowledgments

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Supplementary Material

Supplementary material related to this article can be found at <https://doi.org/10.1016/j.anbehav.2018.07.002>.

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