



Forest elephants: fission–fusion and social arenas

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Fission–fusion systems provide models for studying grouping decisions and social complexity in a range of taxa, as individuals act to manage risks and enhance reproductive success. African savannah elephants, *Loxodonta africana africana*, live in a fluid society where individual relationships persist over decades and affect reproductive success. Social structures have yet to be fully characterized for forest elephants, *Loxodonta africana cyclotis*. Aggregations at natural forest clearings, which are frequent in this subspecies, may offer social benefits in addition to nutritional resources. We examined the social functions of aggregations in Odzala–Kokoua National Park, Republic of Congo. We tested whether clearings function as ‘social arenas’ by examining how social opportunities affected the timing and duration of visits, and how short-term grouping decisions were affected by age, sex, group size and number of elephants present. Aggregations reflected a fission–fusion society similar to that observed in savannah elephants. Grouping patterns were largely unaffected by the number of elephants present, from which we infer that elephants were not acting to minimize competition. Social opportunities affected visit patterns such that visits were longer when others were present. Social opportunities were maximized by joining large groups, often including older elephants, or, for males, parties with females. Large and dynamically changing social groups in clearings offer potential for information exchange and the maintenance of social relationships. Demonstrating that fission–fusion operates in forest elephant society allows future research to focus on cost–benefit modelling, to understand the fitness consequences of these groupings. © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Historically fission–fusion, that is, the flux in temporal patterns of association among individuals who maintain long-term relationships with a number of others, has been considered to be a modal type of social organization for group-living species under weak predation pressure (van Schaik 1989). Fission–fusion grouping patterns are characterized by forming temporary subunits or ‘parties’ that vary in size, composition, cohesion and duration within a model of socioecological constraints (Wrangham 1980; van Schaik 1989). However, a ‘fission–fusion societies’ perspective, which categorizes taxa as either cohesive or as fission–fusion, obscures intermediate grades of group cohesion (Strier 1989), and fission–fusion is now recognized to be both more widespread and more complex in the decisions that underlie grouping patterns than previously thought (Aureli et al. 2008). These decisions occur at the level of the individual and depend on the state and status of the decision-maker, as well as the availability of associates and their states and status. Many ungulate species exhibit temporary large aggregations (Jarman 1974) and sexual

segregation (Conradt & Roper 2005) in the contexts of predator avoidance, infant protection and possibly foraging information exchange. Social carnivores also exhibit fission–fusion, balancing competition against the needs of cooperative hunting and infant and territorial defence (Packer et al. 1990; Creel & Creel 1995). A number of colonially nesting bird species, bee-eaters, weavers, jays, crows, jackdaws and parrots, appear to forage in fission–fusion flocks (Brown 1974; Wanker et al. 1998) to maximize information exchange and minimize predation (e.g. Chapman et al. 1989; Brightsmith & Villalobos 2011). Some of these species also appear to show sex- and age-specific association patterns for social information exchange via play (Bond & Diamond 2004).

African savannah elephants, *Loxodonta africana africana*, provide an excellent model system for studying grouping decisions as they live in multitiered fission–fusion societies with stable multifemale kin units (called families) and gregarious but independent males (Douglas-Hamilton 1972; Moss & Poole 1983; Whitehouse & Hall-Martin 2000; Wittemyer et al. 2005; Moss et al. 2011). Stable dominance hierarchies exist for both males and females; these are size dependent and thereby age graded, and are transitive but not nepotistic within family units (Poole 1987; Archie et al. 2006; Wittemyer & Getz 2007). The complex nature of savannah elephant society has been described as a nested series of social circles (Moss

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1981), or as a molecular structure (Wittemyer & Getz 2007), with a female and her dependent offspring at the centre encompassed by a series of progressively larger circles, representing family units (average size two to six adult females and dependants), bond groups (two to five associated families), clans (geographically contiguous families) and ultimately much of a regional population. Each individual's relationships incorporate individuals beyond the family group (Moss & Poole 1983; McComb et al. 2001) and individual experience and social relationships have long-term implications for fitness and reproductive success, for example calf rearing, response to predators or engagement in high-risk activities such as crop raiding (Lee & Moss 2011; McComb et al. 2011; Moss & Lee 2011a; Mutinda et al. 2011; Chiyo et al. 2012). Female Asian elephants, *Elephas maximus*, have a similar molecular structure to their smaller units, expanding to a series of consistent associates in larger aggregations (de Silva et al. 2011), although the nature of male relationships remains unknown and fitness consequences for females have yet to be determined. Since both genera of elephants exhibit a molecular social structure with fission–fusion decisions at the core of their sociality, fission–fusion may be an ancestral and shared derived 'elephant' trait.

Savannah elephants use fission to minimize competition and fusion to maintain social relationships and gain access to experienced (older) individuals who function as repositories of social and ecological knowledge (sensu McComb et al. 2001, 2011; Evans & Harris 2008; Moss & Lee 2011a). Among forest elephants, *Loxodonta africana cyclotis*, inhabiting the Congo Basin social dynamics have been only briefly described (Turkalo 1996; Payne 2003) and no model of sociality has yet been empirically demonstrated. Resource availability has consequences for party sizes in other fission–fusion taxa such as spotted hyaenas, *Crocuta crocuta* (Kruuk 1972) and chimpanzees, *Pan troglodytes* (Newton-Fisher et al. 2000), and seasonal fluctuations in food and water affect savannah elephant groupings (e.g. Mutinda et al. 2011). The ecological pressures experienced by elephants in the lush equatorial rainforests are very different to those typical for savannah elephants; water is unlimited and fruit, a dietary staple for forest elephants, is patchily located in both time and space (Powell 1997; Blake 2002). Forest elephants in Central Africa tend to range in small groups (approximately three individuals; Morgan & Lee 2007) and, like savannah females, genetic evidence suggests these small groups are most likely to be first-order maternal relatives (Munshi-South 2011). Central African elephants frequently aggregate in natural forest clearings, and these aggregations have been postulated to offer social benefits (Turkalo & Fay 1995) in addition to nutritional resources (Klaus et al. 1998). These 'social arenas' (White et al. 1993; Fishlock et al. 2008) would be fundamental for providing the aggregation opportunities necessary for any fission–fusion system. In forest elephants, juveniles of both sexes disperse from the natal group (Turkalo & Fay 2001) and incur the social costs associated with dispersal, including aggression from strangers, loss of alliance (maternal) support and the time and energy involved in establishing new relationships (Isbell & van Vuren 1996). Elephants could potentially mitigate these costs by using clearings to establish new or maintain existing relationships. Association patterns between forest elephants can be consistent over time and forest elephants show some degree of preference for certain companions (Fishlock et al. 2008) but no study has yet assessed dynamic changes in groupings or social choices. Demonstrating whether forest elephants use clearings to maintain their relationships will allow us to understand how elephant social relationships vary across the wide range of ecological conditions occupied by both forest and savannah elephants.

Our goal in this study was twofold, first to test whether clearings are social arenas for forest elephants and, second, to test whether

forest elephants exhibit similar social structuring to savannah elephants when using these areas. We tested whether clearings function as social arenas by examining how opportunities for social interaction (social opportunities) affect the timing and duration of elephant visits to a forest clearing. We examined elephants' short-term spatial decisions to associate with conspecifics and how these are affected by the size of groupings, the number of elephants using a clearing and the age and sex of individuals and their social partners. Finally, we assessed whether age and sex, fundamental organizing principles governing savannah elephant relationships, also structure forest elephant sociality. If clearings are social arenas, we predicted first that if elephants maximize social opportunities rather than minimize competition, visiting and grouping patterns (short-term spatial associations) should be unaffected by the absolute number of elephants present. This expectation underlies our subsequent predictions for grouping behaviour. Second, elephants should modify their visits according to the social opportunities that they experience, and stay longer in the clearing if they have the opportunity to exchange information with conspecifics. As social rather than foraging exchanges, these should be restricted to the clearing so that the composition of foraging/ranging parties (defined as elephants that arrive and leave the clearing together) should remain largely unchanged. Third, we predicted that groups formed within the clearing should be larger than the mean of ranging parties, and elephants should tend to join parties larger than their own current party in order to maximize social opportunities. For savannah elephants, relationships and information exchange are fundamentally structured by the age and sex of individuals; if the elephant fission–fusion model is ancestral and not derived, we expected age and sex to be important structuring elements for forest elephant relationships also. Finally, therefore, we predicted that associations outside a ranging party should be structured by age and sex.

METHODS

Study Site

Direct observations of forest elephants were made between July 2007 and June 2008 at the Maya Nord clearing (0°46'29.455'N, 52°29'24.078'E) in Odzala–Kokoua National Park, Republic of Congo. High annual rainfall (>1500 mm) peaks in October and March–May (Hecketsweiler et al. 1991). At the time of the study, Odzala–Kokoua was estimated to support 11–18 000 elephants (Blanc et al. 2007). The Maya Nord clearing covers 22.9 ha and is dominated by low-growing vegetation from the Cyperaceae and Poaceae families (Vanleeuwe et al. 1998; Magliocca & Gautier-Hion 2002). Elephant activity is concentrated around two pools in the clearing connected by a series of permanent streams that serve as the principal elephant paths into the clearing. The clearing is surrounded by primary forest in a 1–2 km wide band, outside which lie large areas of dense Marantaceae forests, characterized by an open canopy and a closed understory invaded by *Haumania liebrechtsiana* (Lejoly 1996; Vanleeuwe & Gautier-Hion 1998).

Elephant Observations

Observations were made from 0530 to 1730 hours from a platform located at the forest edge on 187 observation days over 12 months. The distance from observers to elephants averaged 300 m and varied between 90 and 500 m; visibility was generally good. Elephants were unaware of our presence and when they became aware, they would usually flee. Occasions when elephants fled were excluded from analyses. Observers made 30 min counts of all elephants present in the clearing throughout the observation

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