



African Elephant Play, Competence and Social Complexity

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Abstract - Play in African elephants (*Loxodonta africana*) is a life-long activity, with both males and females engaging in a variety of forms of play into their 40s and 50s. Play represents a potentially enriching social and physical activity for elephants, but also one with energetic costs and other risks. Having followed a cohort of individually recognized elephants from birth to adulthood in Amboseli, Kenya, we suggest here some long-term consequences for the role of play in the development of social and physical skills in elephants. Playful elephant calves appeared to be individuals with greater capacity to resist growth insults or stresses and had a reduced risk of dying as adults. The sexes differed in the social contexts and consequences of their early play experiences. Juvenile males used play as a mechanism to enable relaxed contacts with relative strangers, providing vital physical and behavioral information about future friends, associates and reproductive competitors. Females, by contrast, used play as one of the many mechanism for sustaining their social, protective and leadership roles within families.

Keywords - Early experiences; Survival consequences; Sex differences in play, Energetics

Play remains a behavior of considerable fascination, even though we lack a detailed understanding of play's costs and consequences during the developmental period or for later life. Positive immediate physiological and psychological benefits of play can be demonstrated for infants and juveniles, such as enhanced motor-training and neural connectivity (Pellis, Pellis, & Bell, 2010) and the development of social skills such as turn-taking or dominance acquisition (Lee, 1983). Play acts as an additional stimulus for managing social and environmental unpredictability (Spinka, Newberry, & Bekoff, 2001) and provides opportunities for seeking out novelty through a process that Wood-Gush and Vestergaard (1991) called "inquisitive investigation." Play, through investigation and interaction, thus enhances the capacity to manage responses to the unexpected.

Along with these benefits, however, come costs. While not always energetically demanding, play disappears at the first sign of energy or social stress (e.g., Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002). Play is also a high-risk interaction, as demonstrated by observations of injuries or predation attempts during play (Harcourt, 1991), while chimpanzee infants who played more were more likely to contract Ebola (Kuehl, Elzner, Moebius, Boesch, & Walsh, 2008). Play still has direct survival benefits for some juveniles; brown bears that played more had higher early survival, independent of maternal care (Fagen & Fagen, 2009).

Given the debates about the diverse functions of play at various ages and for a plethora of species (e.g., Burghardt, 2005), it is not surprising that we have so few unambiguous examples of play's consequences beyond the juvenile period. Therefore understanding the expression of play in a range of cognitively complex and long-lived species such as parrots (Diamond & Bond, 2003), primates (Palagi, Cordoni, & Tarli, 2004), dolphins (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006) and elephants might help us to determine whether any longer term benefits exist. For species such as elephants, the very

length of their lives and the complexity of accumulated experiences over a lifespan suggest that whatever play's functions might be – immediate or delayed – detection of consequences could be difficult. We have an opportunity in our long-term study of the Amboseli elephants to explore some possible outcomes of play behavior: immediate in relation to energy limitations during drought periods and long-term in relation to longevity and onset of reproduction. Much of what we report here relates to a relative brief developmental window of the first two years of life, during which African elephant calves are highly dependent on their mothers, socially and energetically. Poor energetic conditions (e.g., droughts) and reduced growth during this critical early window have enduring consequences for later survival and reproductive success (Lee, Bussière, Webber, Poole, & Moss, 2013). We use the term “quality” to describe an individual's capacity for sustained growth and to engage in normal activities, as well as to define differences in survival and reproductive potential (see Lee et al., 2013).

We present a description of early play and its associations with other behavior in early life for African elephants. We use our detailed observations of individuals over the past 40+ years to draw a portrait of the ways in which play may influence social knowledge, social competence, and social success for both male and female elephants.

Subjects and methods

The Amboseli elephants

The elephants living in and around Amboseli National Park, Kenya, are individually recognised by natural markings on ears and bodies and the life histories of these individuals have been followed since 1972 (see Moss, Lee, & Croze, 2011). The population has increased in size from ~500 to ~1500 over time, and now consists of 63 distinct family units (female-led kinship groups; Archie et al., 2006) ranging in size from 2 to over 50 individuals and with more than 380 independent males. Males born into families disperse between 10-16 years of age; some remain within the Amboseli population while others disperse into adjacent populations (Chiyo Moss, & Alberts, 2012; Lee & Moss, 1999). We have been working with individuals from this population for an extended period; we therefore present anecdotal evidence about play states and play activities across the sexes and older ages where we lack quantitative analysis, and incorporate these observations into our detailed observations of play in early life.

Play observations

Observations of elephant play were made in the course of a systematic study of elephant calf development and additional observations of events of play behaviour over a 35-year period. The systematic study took place from 1980-1984 on calves between birth and 5 years old; it consisted of 1587 scan samples and 136 hrs of focal observations on 58 males, and 1731 scans samples and 146 hrs of focal observations on 73 females. In the focal samples, all calves were unearned until the birth of their subsequent sibling and all but two 5-year-olds were still attempting to suck. The focal samples were used to relate concurrent activities within each hour-long observation; most calves had two focal samples at different ages, and thus no calf was likely to disproportionately skew the mixed cross-sectional, longitudinal sample. Scans were instantaneous records of mutually exclusive activities when elephants were first encountered and therefore scans of play represented events without durations. Scans and focal samples recorded both the type of play and the age and sex of partners, while focal samples incorporated durations and sequences. Between 1989 and 1994, we carried out 611 further scans on 84 males aged 10-16 years who were in the process of dispersing from their natal families, and recorded all interactions and activities. We have expressed scan data as percentages of play for each age-sex class as individuals were scanned opportunistically. Age classes are defined here as: 0-24 month = young calves; 25-59 months = older calves and juveniles; 5-9.9 years = old juveniles / adolescents; 10-14.9 years = adolescent / young adult 1A; 15-19.9 = young adult 1B; 20-24.9 = adult 2; 25-34.9 = prime adult 3; 35-49.9 = older adult 4; 50+ = old adult 5. The cohort of individuals that was systematically observed has been followed since

1980 so that consequences of early behaviour for subsequent outcomes such as age at first reproduction and death can be examined.

Focal sample data were analysed by individual, using general analysis of variance, plus vicariate and partial correlations on log-normalised hourly rates of occurrence and on the percentage of observations spent in different activities. Where we detected a significant association between age and rates, we ran subsequent analyses on the unstandardized residual values from the regressions in order to explore individual variation controlling for the age at which they were sampled. Cox's proportional hazards survival analysis compared longevity between categories of playfulness, accounting for right censored data. All analyses were carried out in SPSS v19 (IBM Corp).

Results

Age, sex and energy effects on play

Play in elephants is seen from a few weeks of age up to prime and older adult age classes (Figure 1), and in both sexes. Elephants play in a variety of ways (Table 1), which change with age and differ in type between males and females. The percentage of all activities that were social or object / lone locomotor play was similar for young calves at 5-6% of time spent in each type of play in the first year of life; lone play tended to be infrequently observed among the older juveniles (< 1%), but object play persisted into adulthood. Most social play, at all ages, consisted of energetic, escalated interactions (48-100%, mean = 72.1%) such as trunk wrestling, pushing, mounting and chasing between two, three or occasionally, more calves. The relative proportions of escalated and gentle play did not change markedly with age, although gentle play was most common in the first year of life. High intensity contact play was usually with age-mates; gentle play was less common and was more typical of play between older juveniles and the youngest calves.



Figure 1. Two 30+ year old males engaging in wrestle play in a mud wallow

Table 1

Types of Play and the Age-Sex Classes that Engage in this Play Most Frequently

Type of Play	Description of play	Age-sex classes
Active solicitation (alone or in combination)	Tusking ground, kneeling invitation, trunk curl over tusks with head back, trunk raised (spar invitation), waggle head.	All ages; adolescent and adult males (spar)
Environmental exploration	Approach, chase or vocalize at objects (birds, monkeys, other species) in the environment typically with exaggerated movements of the head, trunk and body and often with trumpeting vocalisations. Occasionally can become aggressive.	All ages
Object play	Exploring objects with trunk, mouth, tusks or feet in a vigorous manner; throwing objects, rolling objects, general intense manipulation of objects.	All ages
Lone locomotor play	Running, swinging head, or head low in mock charge. Spinning, rocking, kicking. Often accompanied by “play” (low, pulsating) trumpets.	All ages
Tactile play	Play with mud or water, dust, vegetation or other tactile stimuli; Swimming play with or without contact (e.g. ducking, wrestling in water).	All ages, swimming especially seen in adolescent and adult males
Gentle contact play and Allomothering play	Climb upon, lean on, rub against, roll onto, shove gently, trunk twining and gentle trunk wrestle.	Infant and juveniles, often older juvenile females play with young calves
Escalated contact play, Sparring	Mount, chase, push vigorously, and vigorously spar head to head. Trunk in relaxed position.	Juvenile and adolescent males and females, adult males

The total time spent in play activities declined significantly with age ($r = -0.233$, $n = 282$, $p = 0.002$) with a peak in play rates early in life (Figure 2), and with no significant difference between males and females in hourly rates of play ($F_{1,281} = 2.56$, $p = 0.11$, NS). Although there were no sex differences in play rates, there were some qualitative sex differences; female play rates increased markedly after 48 months when typically there would be either a new sibling to play with or another new calf available in the family.

Since play was at least potentially an energetically costly activity for elephants, we explored the effects of energy availability on play via measures of intake from suckling and from the independent feeding of calves. Age-related declines in play rates were mirrored in suckling frequencies, but suckling and play rates were unrelated ($r = 0.054$, $p = 0.47$, NS; see Figure 2). Controlling for the effects of age-related declines in both suckling and play, there was still no underlying association between these calf activities ($r = -0.012$, $n = 173$, NS). This lack of an association suggests that the energy derived from maternal lactation was unrelated to play frequencies, which was unexpected given that lactation in the first two years of life underlies variation in growth rates and individual survival (Lee et al., 2013). Comparing rates of sucking and play in only the first two crucial years of life still found no major association ($r = 0.066$, $n = 131$, NS). In addition we detected no relationship between maternal control of suckling frequencies (rejections as a proportion of all suckling terminations) and rates of play ($r = 0.094$, $n = 156$, NS).

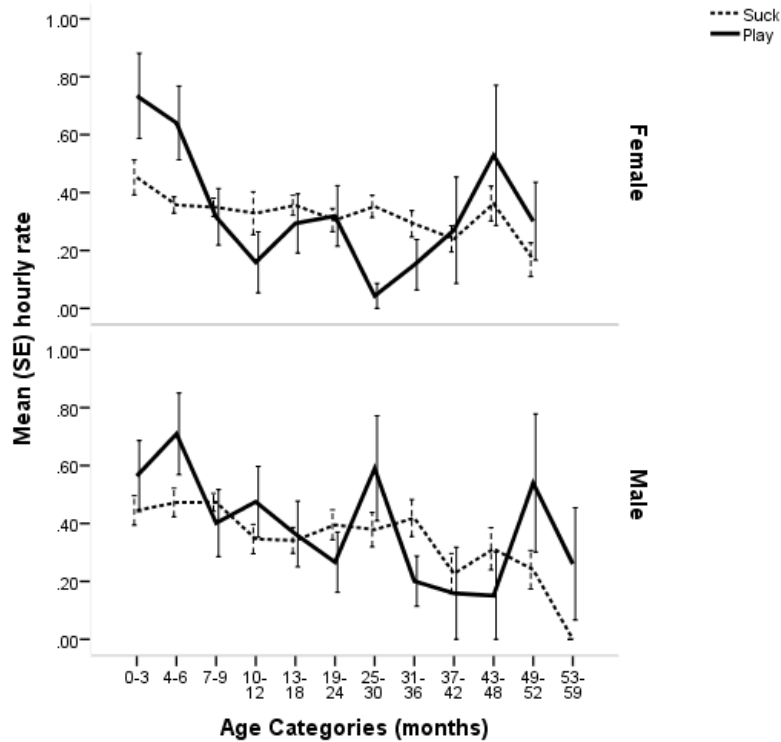


Figure 2. Hourly rate (log \pm SE) of suckling and play for female and male calves from birth to 6 years of age.

Time calves spent in independent feeding increased with age, and negatively co-varied with play ($r = -0.241$, $n = 131$, $p = 0.006$; Figure 3). For older calves, no clear relationship was apparent ($r = 0.089$, $n = 46$, NS; Figure 3A) while in the first two years of life, calves that had the lowest age-specific rates of feeding had higher rates of play ($r = -0.193$, $n = 130$, $p = 0.027$, Figure 3B) suggesting that these playful calves were buffered against at least some of the energy costs of play. After this age, there was again no apparent relationship between rates of play and age-specific energy intake. Were older calves in a state of high energy balance such that our crude indicator of time spent in independent foraging was no longer detecting any relationships? This association remains to be tested.

A small proportion of play observations ($n = 53$) were made during a period of drought – the effect of drought-limited energy on rates of play was clearly shown for both older and younger calves ($F_{1,182} = 15.57$, $p < 0.001$; Figure 4). While younger calves showed a greater reduction of play for age during the dry period than did the older, independently feeding calves, this difference was not significant.

Did the individual variation in play rates bear any relationship to long-term consequences for survival or reproductive success? There was an association between rates of play for calf age and probability of death (Table 2), such that those individuals who played at lower rates than was predicted for their age were more likely to be those who died after the age of 5, by comparison with survivors (Hochberg post hoc $p < 0.014$) and those who died under 5 ($p < 0.045$). Excluding dry year samples which had reduced play and survival, mean survival for less playful calves was 19.9 years (95% CI = 16.8-23.1) by comparison to the more playful calves with an average age of survival of 23.6 years (95% CI = 20.4-26.8; log rank $\chi^2 = 5.26$, $p = 0.022$).

At this stage, we can compare the age at first birth with early rates of play for 73 females and age at first musth (male reproductively competitive phase) for 61 males. There was no relationship between play rates and the onset of reproduction for either sex ($F = 0.016$, NS). Although we find clear signals of individual growth in the age of the onset of reproduction (Lee et al., 2013), a similar signal of reproductive quality was not apparent in these play data.

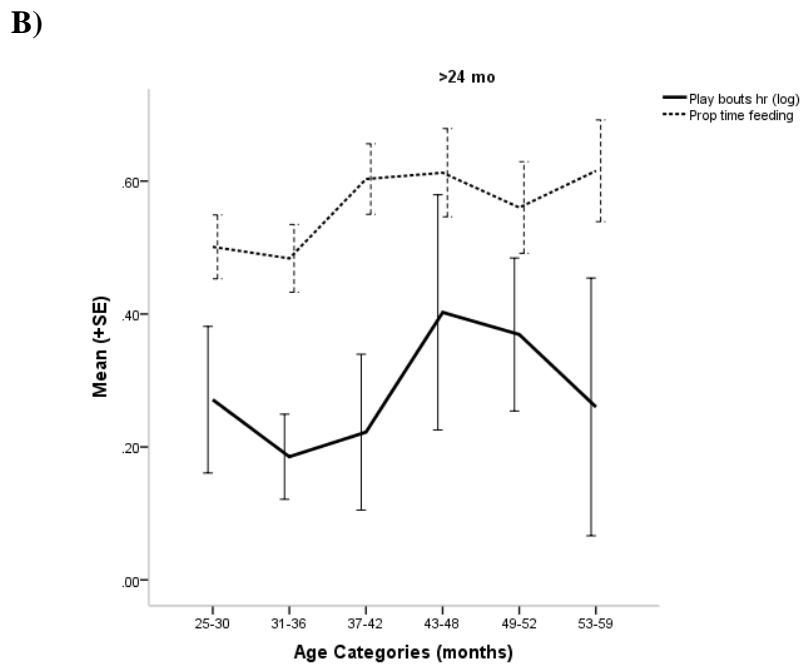
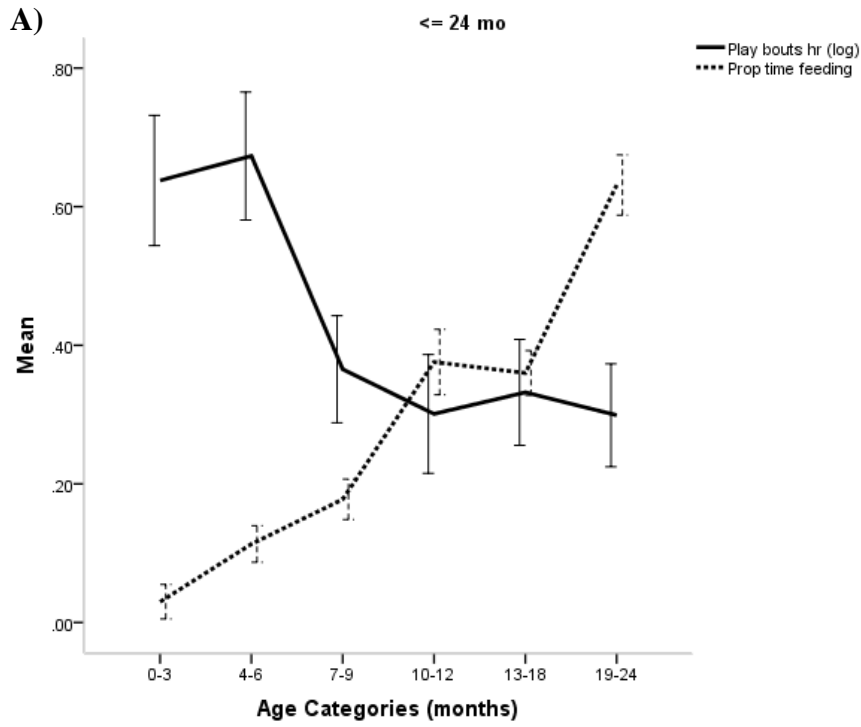


Figure 3. The relationships between the mean (\pm SE) proportion of time spent in independent feeding and rates of play for calves (A) \leq 24 months and (B) $>$ 24 months of age.

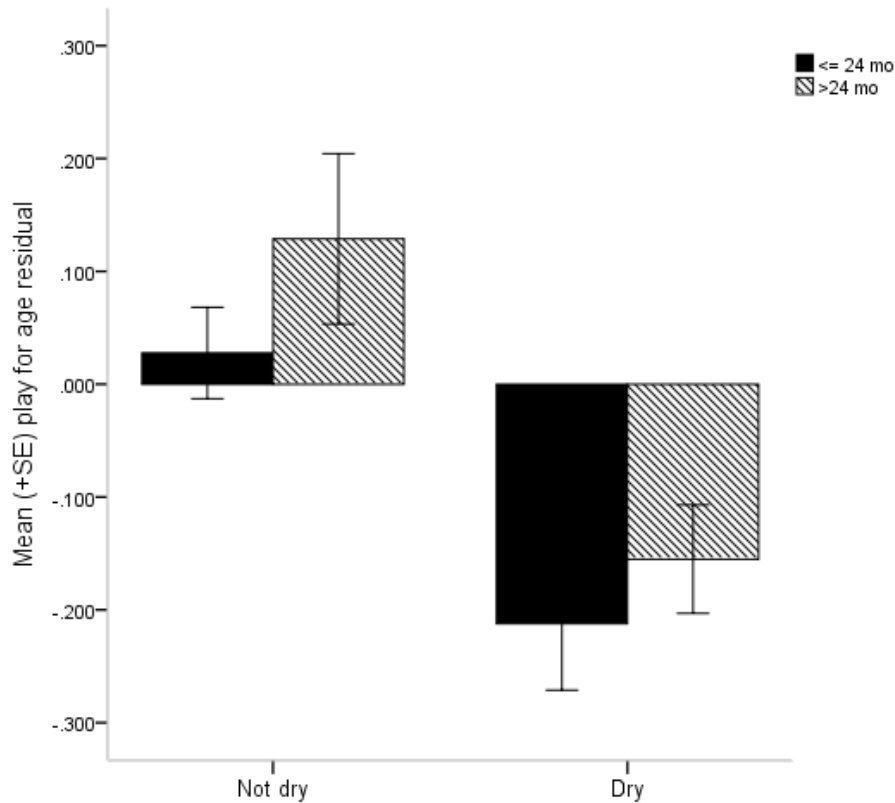


Figure 4. Age-corrected rates of play (residuals \pm SE) compared between drought and non-drought periods and between younger and older calves.

Table 2

Age-specific Play Rates for Calves that Survived for 25+ Years, Calves that Died Before Completed Weaning, and Calves that Died After Weaning

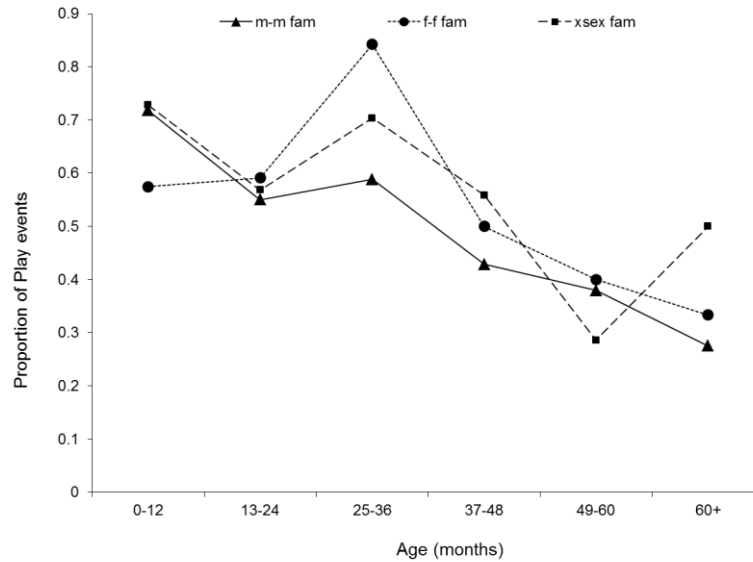
	Calf survived 25+ years	Calf died < 5 years	Calf died > 5 years
Mean residual of play rate			
for age	0.02032	0.01839	-0.19576
(\pm SE)	(± 0.03749)	(± 0.06718)	(± 0.04730)
N	179	50	53

Partner preferences and social novelty

In the first year of life, both male and female calves played for an average of 70.5% of their bouts with members of their own families. As they aged, the percentage of play bouts that were with unfamiliar individuals increased, especially among males (Figure 5). In order to find novel partners, calves had to leave the close proximity and security of their family and initiate play with unfamiliar peers often at considerable distances from their own family members. Since calves and juveniles spent between 80-90% of time within 5m of another family member (Lee, 1986), moving further away represented a context of potential risk, such as the loss of the rest of their family during group movements. Encounters with non-family peers could only occur during those occasions when their family was in an aggregation with less familiar families, representing limited opportunities as well as potential risks. During the period of this study, families spent on average 62% (range 21-98%, $N = 30$) of their time in groupings where other

families were also present (see also Moss & Lee, 2011). While opportunities for encountering less-familiar play partners varied as a function of family size, since larger families tended to be less gregarious, all the focal calves had frequent opportunities to explore and interact with “strangers,” and males were more like to take advantage of these opportunities.

A)



B)

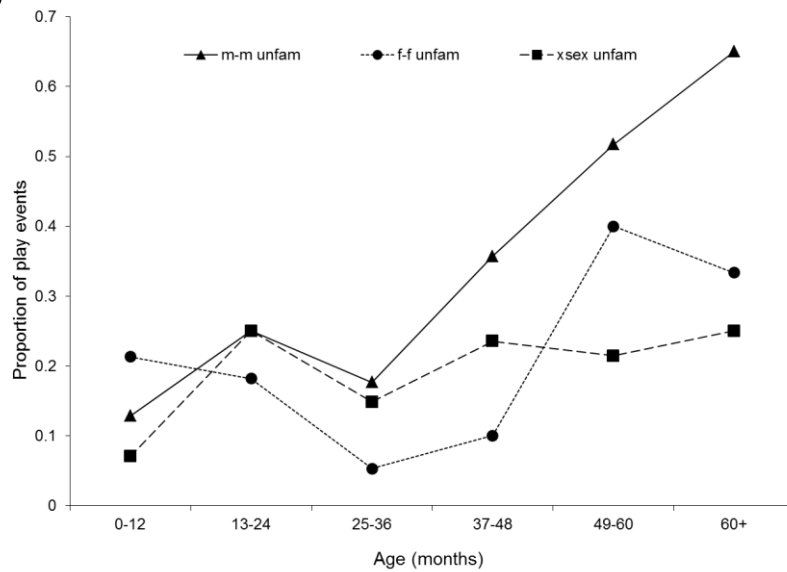


Figure 5. The proportion of play partners that were matched for sex and familiarity; (A) Family partners, (B) Unfamiliar non-family play partners (m-m = male play with male; f-f = female play with female; xsex = across sex; fam = family; unfam = unfamiliar).

Play in adult males

Once males have dispersed from their natal family, they either take up residence in areas away from the core areas of females including those of their mothers (“bull areas”; Moss & Poole, 1983) or they disperse out of familiar habitats into novel areas with strange males and females. The males that have

been continuously observed in our studies tended to have one significant associate – what we have elsewhere called friends (Poole, Lee, Njiraini, & Moss, 2011). Associates, who are not necessarily males from the same family but are often close in age, support each other during high-risk occasions (e.g., crop-raiding, Chiyo et al., 2011), and they tend to be the most frequent play/sparring partners of each other.

The nature of a male's relationship with his peers underlies his early dispersal decisions (Lee & Moss, 1999); males with friends may be able to leave their families early as a result of social support while they establish new home ranges. We suggest that adolescent and young adult males (aged 10-19) use play as a mechanism to test the physical capacities and trustworthiness of potential friends. Among older males, play cements existing bonds which can lead to reduced mate competition by spacing out musth periods between associates (Poole et al., 2011). Play was however relatively rare during the process of independence; 1.6% of the 611 young male scans were of males interacting with others (play, sparring, gentle friendly contacts), compared with 3.7% of activities that were play for 5-9 year old males.

Adult male-male play typically consists of sparring (see Figure 1), but in water, males will engage in a variety of types of contact (ducking, wrestling, mounting). Both trunk reaching and tusking the ground are used by adult males as signals of play intention or invitation. While we do not have frequencies for these events, we can suggest that it is important for males to use unambiguous signals of playful intent since escalated non-playful sparring (fights) can result in serious injuries (Poole, 1989). Sparring between friends appears to be more relaxed than that between strange males, but may escalate into more aggressive bouts with the use of tusks and charges resembling those in serious male-male fights. Although quantitative data again are lacking, we can suggest that when two males are engaged in sparring associated with the following forms of relaxed contact – trunks entwined or trunks touching each other's bodies and especially the other's mouth, with heads low and ears dropped – the interactants are likely to be familiar partners. Males will play with objects in the environment such as vehicles (bouncing them on their springs, rocking them by gently pushing them backwards and forwards) and they use trunk position and ear and body postures as signals that indicate that their intentions are playful. Whether they are playing with the people inside (who may not appreciate these acts as “playful”) or playing with a large metal object remains to be determined. Other occasions of adult male play consist of brief bouts of chasing other species, with characteristic floppy head shakes, or relaxed trunk and foot manipulation of objects in the environment, such as branches or clumps of plants, where the intention is clearly not to eat these objects but to throw them around at random.

Do males play with females and calves? Such play has only rarely been observed in Amboseli. Young males and females (e.g., 10-19 year olds) from different families may spar after a vocal or affiliative contact greeting, although these play bouts appear to be shorter than those between males. Males are also tolerant of calf play and while they might not join in, they will allow play events to occur all around them. We have yet to observe a male become impatient with the presence of juveniles playing near him.

Adult female play and personality

Our analysis of immature play above suggested that female play was more focused on family or familiar partners as well as engaging in gentle play with younger, vulnerable calves – what we call allomothering play (Table 1). However, females of all ages play when conditions are good (high energy availability, many infants, large aggregations). In large groups in particular, adult females and even matriarchs, will engage in lone locomotor play (floppy head running), vocalising (play trumpets) or object play (e.g., with vegetation). They will also gently trunk-touch younger animals who are playing and invite further physical contact.

We found that a key trait for elephant personalities, emerging from an analysis of a very small number of individuals in a single family, was “leadership” and the second personality component that emerged was “playfulness” (Lee & Moss, 2012). Human perceptions of adult female playfulness were somewhat related to the female's age with the oldest female ranked as least playful, and inversely associated with within-family traits of leadership and confidence (Figure 6). All the females in the

personality sample were reproductively active, suggesting that playfulness was a variable trait of individual activity levels and personality that stretched far into adulthood for female elephants. We have yet to determine if individual female playfulness in adult life relates to family propensities to be gregarious, if more playful females are of higher quality, as was suggested by the analysis of mortality risks above, and therefore whether playful families are more reproductively successful, or if playfulness is simply a generalised elephant characteristic whose influence on sociability, survival and reproductive success forms part of a behavioural package for all adult elephants.

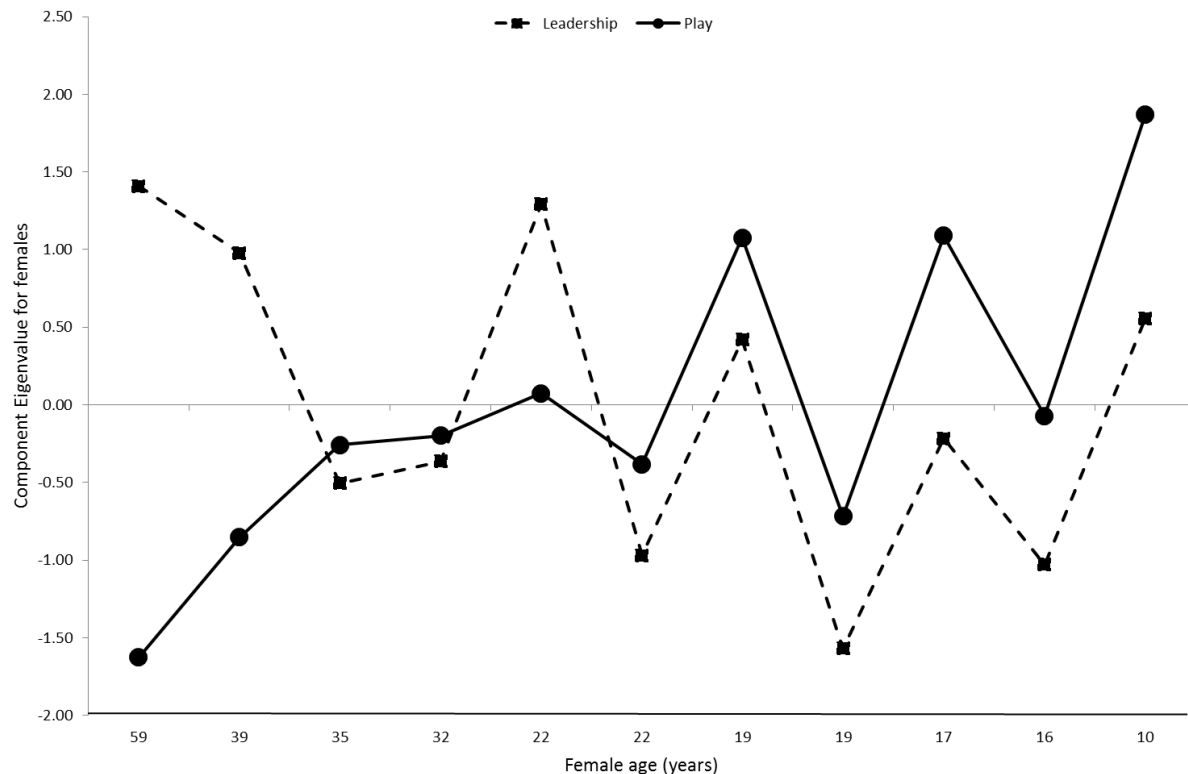


Figure 6. Playfulness, leadership and age in one family of elephants: personality characteristics of adult females (from Lee & Moss, 2012).

Discussion

Elephant sociality, survival and play are inextricably linked; play in early development appears to be a good indicator of individual quality (the capacity for growth, survival and reproduction; Lee et al., 2013) in later life. In addition, play's role in training individuals for the unexpected in their physical and social environments (e.g., Kuczaj et al., 2006; Spinka et al., 2001) allows male elephants to experience diverse novel social partners that are lacking in their family groups during early development and possibly unavailable once males disperse and become more solitary. The importance of seeking out novel age-mates in order to provide social opportunities that are not available via normal associates has been demonstrated for other fission-fusion species such as dolphins (Kuczaj et al., 2006; Paulos, Trone, & Kuczaj, 2010) and probably also operates in chimpanzees (Hayaki, 1985). For male elephants, allowing for potentially dangerous contacts in the low risk, high arousal state of play may provide an enriched environment for risk-learning and indeed for the reinforcing value of risky experiences themselves (e.g., Burghardt, 2005; Miller & Byers, 1998). For female elephants, some level of playfulness remains an individual characteristic into old age alongside other personality traits such as leadership, gentleness and

constancy (Lee & Moss, 2012). Leadership and play co-vary for younger female family members, suggesting that playfulness was an indicator of popularity, competence and sociability that was accorded some value by other family females, and therefore may reflect a female with leadership potential.

Play, as has been shown for a range of species (e.g., primates: Baldwin & Baldwin, 1974; Lee, 1984; Sommer & Mendoza-Granados, 1995; ungulates: Krachun, Rushen, & de Passillé, 2010; Miller & Byers, 1991; ground squirrels: Nunes, Muecke, Anthony, & Batterbee, 1999; meerkats: Sharpe et al., 2002), is an excellent measure of environmental conditions. Play rates decreased markedly during droughts, although we were unable to detect a direct correspondence with energy intake through suckling or independent calf feeding. Our measures of intake were however very crude and therefore only likely to represent gross patterns. We anticipated that play might be used as a mechanism to cope with weaning stress (e.g., Donaldson, Newberry, Špinka, & Cloutier, 2002), but there was no clear correspondence between play and our measures of maternal control of suckling attempts despite the observation that suckling control was predictor of maternal weaning strategies (Lee, 1986; Lee & Moss, 1986). Overall, playful elephants were those that fed independently for less time in their first two years of life, suggesting that they were buffered against energy costs of play. Similar to sea lion pups observed during an El Niño event (Ono, Boness, & Oftedal, 1987), maternal food limitations during droughts were associated with early calf mortality, poor growth rates and reduced lifetime fitness (Lee et al., 2013) and during these drought periods, calves played far less even when they survived these early stressors.

Play rates in early life were associated with the risk of mortality after weaning rather than during the peak play period of the first 4-5 years of life. Among brown bears (Fagen & Fagen, 2009), playfulness was positively associated with survival to independence – providing an increase in the probability of survival of between 1 to 9 times that of the effects of food availability and maternal care. While we did not find enhanced pre-weaning survival as a result of play, there was a surprisingly long-term effect. Low rates of play for age in early life may either be an indicator of lower individual quality, or may be associated with reduced growth rates, which act as an additional mortality risk factor (Lee et al., 2013). The sample sizes are however very small and the “excess” deaths occurred over the next 25+ years and for a variety of causes; therefore causality and mechanisms need to be interpreted with caution.

Much remains to be understood about elephant play. Many factors influence the opportunities for social play: demography, through family size and the numbers of other calves of similar ages present in a family or in the population at large; the personality and age of the matriarch, who may be more or less playful and who also determines a family’s tendency to be sociable. Opportunities for lone and locomotor play may be more directly linked to energy availability, but could also vary as a function of predator presence or other landscape risks. At this stage, while we can only speculate about the constraints and opportunities, as well as the consequences of play in elephants, we have demonstrated a fascinating long-term association between play and survival.

Acknowledgements

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References

- Archie, E. A., Moss, C. J., & Alberts, S. C. (2006). The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society Series B*, 273, 513-522.
- Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist*, 14, 303-315.

- Burghardt, G. M. (2005). *The genesis of animal play*. Cambridge, MA: MIT Press.
- Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. *Animal Behaviour*, *81*, 1093-1099.
- Chiyo, P. I., Moss, C. J., & Alberts, S. C. (2012). The influence of life history milestones and association networks on crop-raiding behavior in male African elephants. *PLoS One*, *7*, e31382.
- Diamond, J., & Bond, A. B. (2003). A comparative analysis of social play in birds. *Behaviour*, *140*, 1091-1116.
- Donaldson, T. M., Newberry, R. C., Špinko, M., & Cloutier, S. (2002). Effects of early play experience on play behaviour of piglets after weaning. *Applied Animal Behaviour Science*, *79*, 221-231.
- Fagen, R., & Fagen, J. (2009). Play behaviour and multi-year juvenile survival in free-ranging brown bears, *Ursus arctos*. *Evolutionary Ecology Research*, *11*, 1-15.
- Harcourt, R. (1991). Survivorship costs of play in the South American fur seal. *Animal Behaviour*, *42*, 509-511.
- Hayaki, H. (1985). Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates*, *26*, 343-360.
- Krachun, C., Rushen, J., & de Passillé, A. M. (2010). Play behaviour in dairy calves is reduced by weaning and by a low energy intake. *Applied Animal Behaviour Science*, *122*, 71-76.
- Kuehl, H. S., Elzner, C., Moebius, Y., Boesch, C., & Walsh, P. D. (2008). The price of play: Self-organized infant mortality cycles in chimpanzees. *PLoS One*, *3*, e2440.
- Kuczaj, S. A., Makecha, R., Trone, M., Paulos, R. D., & Ramos, J. A. (2006). Role of peers in cultural innovation and cultural transmission: Evidence from the play of dolphin calves. *International Journal of Comparative Psychology*, *19*, 223-240.
- Lee, P. C. (1983). Play and the development of relationships. In R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp. 81-89). Oxford, UK: Blackwells.
- Lee, P. C. (1984). Ecological constraints on the social development of vervet monkeys. *Behaviour*, *91*, 245-262.
- Lee, P. C. (1986). Early social development among African elephant calves. *National Geographic Research*, *2*, 388-401.
- Lee, P. C., & Moss, C. J. (1986). Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology*, *18*, 353-361.
- Lee, P. C., & Moss, C. J. (1999). The social context for learning and behavioural development among wild African elephants. In H. O. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 102-125). Cambridge, UK: Cambridge University Press.
- Lee, P. C., & Moss, C. J. (2012). Wild female African elephants (*Loxodonta africana*) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology*, *126*, 224-232.
- Lee, P. C., Bussière, L. F., Webber, C. E., Poole, J. H., & Moss, C. J. (2013). Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (*Loxodonta africana*). *Biology Letters*, *9*(2), 20130011.
- Miller, M. N., & Byers, J. A. (1991). Energetic cost of locomotor play in pronghorn fawns. *Animal Behaviour*, *41*, 1007-1013.
- Miller, M. N., & Byers, J. A. (1998). Sparring as play in young pronghorn males. In M. Beckoff & J. A. Byers (Eds.), *Animal play* (pp. 141-160). Cambridge, UK: Cambridge University Press.
- Moss, C. J., & Lee, P. C. (2011). Female social dynamics: Fidelity and flexibility. In C. J. Moss, P. C. Lee, & H. Croze (Eds.), *The Amboseli elephants: A long-term perspective on a long-lived species* (pp. 205-223). Chicago, IL: University of Chicago Press.
- Moss, C. J., Lee, P. C., & Croze, H. (2011). *The Amboseli elephants: A long-term perspective on a long-lived species*. Chicago, IL: University of Chicago Press.
- Moss, C. J., & Poole, J. H. (1983). Relationships and social structure of African elephants. In R. A. Hinde (Ed.), *Primate social relationships* (pp. 314-325). Oxford, UK: Blackwells.
- Nunes, S., Muecke, E. M., Anthony, J. A., & Batterbee, A. S. (1999). Endocrine and energetic mediation of play behavior in free-living Belding's ground squirrels. *Hormones and Behavior*, *36*, 153-165.
- Ono, K. A., Boness, D. J., & Oftedal, O. T. (1987). The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behavioral Ecology and Sociobiology*, *21*, 109-118.
- Palagi, E., Cordini, G., & Tarli, S.B. (2004). Immediate and delayed benefits of play behaviour: New evidence from chimpanzees (*Pan troglodytes*). *Ethology*, *110*, 949-962.
- Paulos, R. D., Trone, M., & Kuczaj, S. A. (2010). Play in wild and captive cetaceans. *International Journal of Comparative Psychology*, *23*, 701-722.

- Pellis, S. M., Pellis, V. C., & Bell, H. C. (2010). The function of play in the development of the social brain. *American Journal of Play*, 2, 278-298.
- Poole, J. H. (1989). Announcing intent: The aggressive state of musth in African elephants. *Animal Behaviour*, 37, 140-152.
- Poole, J. H., Lee, P. C., Njiraini, N., & Moss, C. J. (2011). Longevity, competition and musth: A long-term perspective on male reproductive strategies. In C. J. Moss, P. C. Lee, & H. Croze (Eds.), *The Amboseli elephants: A long-term perspective on a long-lived species* (pp. 272-286). Chicago, IL: University of Chicago Press.
- Sharpe, L. L., Clutton-Brock, T. H., Brotherton, P. N. M., Cameron, E. Z., & Cherry, M. I. (2002). Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour*, 64, 113-121.
- Sommer, V., & Mendoza-Granados, D. (1995). Play as indicator of habitat quality: a field study of langur monkeys (*Presbytis entellus*). *Ethology*, 99, 177-192.
- Špinka, M., Newberry, R. C., & Bekoff, M. (2001). Mammalian play: Training for the unexpected. *Quarterly Review of Biology*, 76, 141-168.
- Wood-Gush, D. G. M., & Vestergaard, K. (1991). The seeking of novelty and its relation to play. *Animal Behaviour*, 42, 599-606.