ORIGINAL ARTICLE

Personality and behavioral changes in Asian elephants (*Elephas maximus*) following the death of herd members

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ABSTRACT

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Elephants are highly social beings with complex individual personalities. We know that elephants have a general interest in death, investigating carcasses, not just limited to kin; however, research does not explore in depth whether individuals change their behavior or personality following traumatic events, such as the death of a conspecific. Within a captive herd of Asian elephants (*Elephas maximus*) housed at Chester Zoo, UK, we measured social behaviour and proximity and personality using the TIPI, and found age-related and relationship-related changes in both behavior and personality following the deaths of herd members. Overall, the herd spent less time socialising and engaging in affiliative behaviors following the death of the adult female when compared to baseline data, yet spent more time engaging in these behaviors after the death of two calves. The death of the central female had a dramatic impact on her infant calf, resulting in increasingly withdrawn behavior, yet had the opposite effect on her adult daughter, who subsequently established a more integrated role within the herd. Emotional Stability fell in the motherless calf but rose in an adult female, who had lost her adult daughter, but had a new calf to care for. We suggest that the greater impact on the behaviour and personality of surviving herd members following the deaths of calves, compared to an adult member, attests to the significance of the unifying role played by calves within an elephant herd.

Key Words

Captive environment, Death, Elephant, Grief, Proximity

INTRODUCTION

Elephants, both Asian (*Elephas maximus*) and African (*Loxodonta africana*) are considered to be highly social beings, with extensive, well-defined and multi-tiered social networks (Archie, Moss & Alberts, 2006; Doyle, 2018; Sukumar, 2006). Herds are genetic units, led by a matriarch, with an

individual's closest and most important social partners being their first-degree maternal relatives; herds are described as being 'female-bonded' (Archie *et al.,* 2006b; Archie, Morrison, Foley, Moss, & Alberts, 2006). The intricate network of bonds and affiliative relationships are maintained via communication, interactive behavior and proximity (Bonaparte-Saller & Mench, 2018; Jayantha, Dayawansa, Padmalal & Ratnasooriya, 2009). Such strong bonds are replicated within some captive settings; captive Asian elephants were observed to spend approximately 70% of their time associating with conspecifics (Petraccione, Root-Gutteridge, Cusano & Parks, 2017).

The complex social behavior of elephants is further evidenced through reunion activities; when individuals are separated and then reunited, they engage in tactile greetings (Moss, 2012). Tactile communication is one of the most frequent forms of contact, within and between elephant herds; contact rubbing during greeting ceremonies is seen as a form of comfort (Archie *et al.*, 2006a; Gadgil & Nair, 1984; Lee 1987). Other affiliative interactions are categorised under trunk-to behaviors, whereby an individual touches the mouth, genitals, face or trunk of another with their own trunk (Garai, 1992). Trunk-to-mouth affiliative behavior is commonly reported; an individual will place their trunk in the mouth of a conspecific or in their own mouth, the latter being synonymous with a human infant sucking their thumb (Vidya, 2014).

The most balanced affiliative interactions are found in the mother-daughter dyad, with most being initiated by the calf (Gadgil & Nair 184; Garai, 1992; Harvey, Daly, Clark, Ransford, Wallace & Yon, 2018). The mother-infant bond is the strongest, the fundamental core of a herd; calves are completely dependent on their mothers, reliant on her for nutrition, protection and comfort (Couzin, 2006; Harvey *et al*., 2018; Lee, 1987). Although there is inconsistency amongst researchers regarding the percentage of time a calf will remain proximal, or rather within 5m of its mother, it is generally accepted that 70-90% of a calf's available time is an accurate range (Lee, 1987; Moss, 2012; Petraccione *et al.*, 2017). Such measures can be viewed as an indicator of relationship strength. Whilst the overarching bond

between a mother and her offspring cannot be disputed, investment in the calf differs based on gender; mothers may permit a higher milk intake from males, potentially because the size of adult males is an important prerequisite in future mating success (Lee & Moss, 1986).

Until recently, there has been a relative paucity in research investigating male sociability. Research has not necessarily ventured beyond stating that, upon maturity, males leave their natal herd joining either a male 'bachelor' herd or remaining solo, opting only to integrate with female herds during the mating season (Chiyo, Archie, Hollister-Smith, Lee, Poole, Moss & Alberts, 2011). Leaving their natal herd is seen as a gradual process taking up to four years (Hartley, Wood & Yon, 2019). Infant males benefit highly from male socialisation for the development of successful reproductive behaviors (Hartley *et al.*, 2019; Poole & Granli, 2009). Often following older musth males, young male elephants spend more time socialising with older males, not necessarily relatives, as opposed to female herd members (Hartley *et al.*, 2019; Poole & Granli, 2009). However, they seldom have the opportunity to socialise in captivity due to problematic practical constraints surrounding housing more than one male, although it is recommended that they should not be translocated until the age of five (Hartley *et al.*, 2019; Schulte, 2000).

Whilst juvenile male elephants have been observed to distance themselves from calves, females in a herd, regardless of age or having offspring of their own, collectively care for the calf; a calf will spend almost all of their time (98%) in close proximity to other herd members (Gadgil & Nair, 1984; Petraccione *et al.,* 2017). This cooperative behavior amongst the female herd members is termed allomothering, a form of mother-like behavior (Lee, 1987; Rapaport & Haight, 1987). Allomothers are often young nulliparous females, maternally related to the calf (Rapaport & Haight, 1987). The primary role of an allomother is to collectively protect the calf from any external threats or social hazards; females have been observed to form an outward facing circle around a calf, an act entitled circular defence (Dublin, 1983; Lee, 1987). Moreover, females respond immediately to a calf's

distress call, with such calls evoking a dramatic response (Gadgil & Nair, 1984). There are conflicting opinions regarding an allomother's role in suckling a calf, with some stating that nulliparous allomothers, when confronted by calves, will allow suckling (Gadgil & Nair, 1984; Vidya, 2014). Contradictory research, however, states that only 3% of suckling attempts are directed to non-mothers and only 26% of these are successful, perhaps because it makes little sense for an allomother to allow it (Lee, 1987). Nonetheless, allomothering is vital in the maintenance of a matriarchal society, with the benefits of allomothering including experience in rearing, shared resources, inclusive fitness and future reciprocation which, despite being a delayed benefit, enhances group stability (Archie et al, 2006; Dublin 1983; Lee, 1987; Schulte, 2000). Such social facilitation, evidenced through their lifelong cooperative relationships, is thought to have evolved in order to aid survival of young, providing further support to the notion of social complexity (Bonaparte-Saller & Mench, 2018; Schulte, 2000; Vanitha, Thiyagesan & Baskaran, 2011).

Such complexity is not merely limited to social behavior; elephants also have complex, and distinct, individual personalities. The study of animal personality can be traced back to descriptions of animals being 'sociable' or 'fearful' – or bold versus shy - as early as the 20th century, although caution must be taken to avoid anthropomorphism (Whitham & Washburn, 2017). The top-down approach to personality measurement, involving the use of a human model to assess animal personality, is regarded as a controversial issue, with criticism that such an approach is inherently flawed, with some traits being harder to identify than others (Weiss, 2017). On the one hand, the Five Factor Model, or Big Five, is regarded as unique to human personality due to the evolutionary benefits of being an Extraverted or Agreeable individual, based on primitive notions of sociability and altruism (Gartner & Weiss, 2018). On the other hand, the Five Factor model has proven able to reliably measure personality in species including chimpanzees, proposed as being most efficient when used to group numerous personality descriptors or characteristics into the five broad traits (King & Figueredo, 1997).

Other research into elephant personality research has used a bottom-up, rather than top-down, approach, often adapting the Madingley questionnaire originally used with rhesus macaques (Stevenson-Hinde & Zunz, 1978): 28-item inventory which, through Principal Components Analysis, produces the components that account for variance and thus best explain personality in the given species (Grand, Kuhar, Leighty, Bettinger & Laudenslager, 2012; Lee & Moss, 2012; Seltmann, Helle, Adams, Mar & Lahdenpera, 2018). Lee and Moss (2012), for example, used a version of this rating scale (adapted by Murray, 1998) to, investigate personality in wild African elephants (*Loxodonta africana*). They found that four components explained their distinct personalities: Leadership, a trait shown most by the matriarch of the herd; Play, an age-related trait; Gentleness and Constancy, associated with effective sociability, linking to predictability of behavior and individual popularity. These findings from a wild African herd, may not necessarily be replicated in Asian elephants (*Elephas maximus*) or their captive counterparts. Different components were identified in the Seltmann *et al.* (2018) study which used an adapted personality inventory targeted more specifically to a working herd of captive Asian elephants; these were Attentiveness, linked to responsiveness to commands, Sociability and Aggressiveness (Seltmann *et al*., 2018). This highlights how researchers should take care when inferring that the findings from captive/wild, or African/Asian elephants, will be the same. Although Asian elephants share several similarities with their African counterparts, possessing social, behavioral and morphological similarities, they also differ, from physical characteristics including their size and ear shape to the structure of their dominance hierarchies (Sharma, Pokharel, Kohshima & Sukumar, 2019).

Research investigating the stability of personality over time is relatively lacking. Dolphins have been found to exhibit consistency across time periods, remaining unchanged even after the destruction of their habitat as a result of Hurricane Katrina and subsequent relocation (Highfill & Kuczaj, 2007). Some previous research on elephants found that personality traits are temporally stable, persisting

across various contexts, over a one-year period (Horback, Miller & Kuczaj, 2013). The only changes observed were attributed to maturational effects rather than actual personality change; juvenile males become more solitary as they age, reflective of their behavior in the wild (Horback *et al.*, 2013). Research has not, however, investigated whether personality changes in response to an important life event such as the death of a companion. Intuitively, it would make sense for the death of a close attachment figure or mate to impact personality traits and behaviors due to the strong social and affiliative bonds integral to an elephant herd (Bonaparte-Saller & Mench, 2018; Vanitha, Thiyagesan & Baskaran, 2011).

It is widely accepted that elephants have an awareness of and a general interest in death (Sharma *et* al., 2019). Male elephants approach the carcasses of other males as a form of dominance, obtaining necessary information about the deceased and engaging in displacement behaviors; female herds have been observed to visit the carcasses of unrelated matriarchs or multiparous females, directly investigating the carcass (Douglas-Hamilton, Bhalla, Wittemeyer & Vollrath, 2006; Hawley, Beirne, Meier & Poulsen, 2018; Goldenberg & Wittemyer, 2019; Merte, Gough & Schulte, 2009). Such interest is not merely limited to kin; African elephants have been observed to direct attention towards dead conspecifics regardless of relationship strength with the deceased (Goldenberg & Wittemyer, 2019). However, it is unknown as to whether there is a difference between a carcass and bones; their extensive investigation of a carcass, occurring at various stages of carcass decay, including sniffing the deceased is seen to represent processing of death (Goldenberg & Wittemyer, 2019; Hawley *et al.,* 2018). This then leads one to question whether without the visual and/or olfactory cues that surround a carcass, an individual would recognise death? This, therefore, suggests that the assumption that elephants have an overarching interest in death may not be completely sound.

Gonçalves and Biro (2018) explored the different cues animals use to detect life and death in others; detecting life via animate/inanimate distinction and detecting death via scent cues, including, but not

limited to, necrophobia, defined as avoidance or aversion to 'death scents'. Many taxa exhibit complex responses, combining tactile cues with scent; elephants have been observed to place their trunk in the mouth of the deceased to attain gustatory information about the carcass combined with the olfactory system, described as an extended sensory experience (Gonçalves & Biro, 2018; Hawley *et* al, 2018). Research has indicated that this interest does extend to bones of deceased conspecifics, elephants favouring them over natural objects or the bones of other species; no preference was shown, however, towards to the bones of a related conspecific compared to an unrelated individual (McComb, Baker & Moss, 2005). McComb *et al*. (2005) claim therefore that reports of an elephant supposedly touching the bones of their deceased relatives can be explained by a shared home-range and their general interest in death.

Such research states only that an elephant has an interest in death, and details typical responses to viewing a carcass or bones; it does not, however, detail any changes resulting from this death or how the death of a conspecific affects those left behind. Research from Sharma *et al*. (2019) pondered that an individual 'might' experience distress following the death of a conspecific but did not delve into a deeper definition of what this distress entails, and whether the deaths of different specific individuals elicits varied responses. Furthermore, elephants have been described as a "who animal", suggesting that who dies, or rather the survivors' relationship to the deceased, matters (Safina, 2018, pp 65). For example, what happens when a mother dies, leaving an orphaned calf? As highlighted previously, calves are completely dependent on their mothers, so, it would be reasonable to suggest that the death of a mother would impact upon the surviving calf. Douglas-Hamilton *et al.* (2006) report how the six-month-old calf of a deceased female only survived a matter of weeks following her death, with unsuccessful attempts at suckling other females observed.

Calves are ten times more likely to die in their first year following the death of their mother, with delayed effects also observed, and are at increased risk of mortality up to the age of four years

(Lahdenpera, Mar & Lummaa, 2016a). This effect is heightened if the mother was older or the calf was male ((Lahdenpera, Mar & Lummaa, 2016a), with male calves having 2.4 times higher a risk of mortality compared to female calves who had lost their mothers, potentially linking to the differing maternal investment based upon calf sex discussed previously (Lahdenpera, Mar & Lummaa, 2016a; Lee & Moss, 1986; Moss, 2012). Overall, only 25% of calves who had lost their mother before aged four lived to twenty-years-old (Lahdenpera, Mar & Lummaa, 2016a). The presence of a grandmother housed with an infant could reduce calf mortality risk by eight times (Lahdenpera, Mar & Lummaa, 2016b). If the calf does not die immediately following the death of its mother, they are still subject to increased aggression, especially during feeding periods, often resulting in herd abandonment (Goldenberg & Wittemyer, 2018). Such findings are also reflected in the similarly social species, chimpanzees; observations of a young male chimpanzee dying three weeks after the death of his mother further supports the notion that infant decline is associated with the loss of an emotional attachment figure (Anderson, 2011). These fates depict the fatal impact of maternal deprivation, yet, remain surprising in the context of closely-bonded social groups observed in species such as chimpanzees and elephants.

Knowing that herds are female-bonded and notable for their high degree of allomaternal care, one would think that the death of a female would have an effect on all herd members, and not be limited just to her offspring. This would certainly be the case if said female was the matriarch; the death of whom can trigger "devastating psychological consequences" (Safina, 2018, pp. 40). Elder African matriarchs' tusks make them desirable to poachers, yet killing a matriarch prematurely leaves the survivors unprepared (Safina, 2018). The matriarch is the central pillar of an elephant community; her knowledge is vital to the survival of the herd, and herds led by more experienced matriarchs suffer less calf mortality (Bradshaw, 2004; Douglas-Hamilton *et al*. 2006). Matriarchs are regarded as the glue that holds the herd together; the loss of a matriarch may ultimately result in herd dissolution (Douglas-Hamilton *et al* 2006). The importance of a leader, and the substantial effect their death has on the surviving group members, is reflected in other species too. In a group of captive gorillas,

although neither affiliative, abnormal nor aggressive behaviors were observed to increase or decrease following the death of the dominant silverback (Gartland, McDonald, Braccini Salde, White & Sanz, 2018; Less, Lukas, Kuhar & Stoinski, 2010), the loss of a well-established individual within a group can still impact remaining group dynamics. The sociability of the deceased individual is seen as a primary factor influencing the reactions of others. Responses to a chimpanzee's death have been shown to be mediated by the age, social history and integration of the deceased (Van Leeuwen, Mulenger, Bodamer & Crown, 2016). If the animal was largely social, chimpanzees responded collectively whereas a less social individual was only attended after death by close family members (Van Leeuwen *et al.*, 2016). In elephants, however, the importance of individual sociability is disputed; as discussed previously, elephants show a general interest in death irrespective of relationship strength with the deceased (Goldenberg & Wittemyer, 2019).

Reports exist that the death of a female, matriarch or not, affects the entire herd and is seemingly worse than the death of a calf, which primarily causes distress for their mother alone (Bradshaw, 2004). Yet, research continually reiterates the importance of a calf in unifying the herd, with some even stating that the needs of a herd cannot be met without the presence of a calf (Schulte, 2000). Therefore, the death of a calf may elicit more significant changes in the behavior of survivors. There is a paucity of research, however, investigating this in elephants. Primates and cetaceans are observed to display highly emotional responses following the death of offspring. Thanatalogical behaviors include carrying and caring for the deceased infant, defined as epimeletic behavior; other behaviors in cetaceans include stationing near the floating carcass or circling it in the water (Anderson, 2011; Bearzi, Eddy Piwetz, Reggente, & Cozzi, 2017; Reggente *et al.,* 2018). Epimeletic behavior can be described as caregiving, with individuals acting aggressively or defensively towards intruders who may remove their dead offspring; observations of cetaceans caring for their dead conspecifics were reported as a single or series of events, seemingly having no long-lasting effects (Bearzi, *et al.,* 2018; Bearzi & Reggente, 2018).

However, these behaviors remain largely unexplained with research lacking quantitative coding. It is unknown as to why some mothers carry their deceased infants for weeks whereas others do not, with environment, such as extreme weather conditions, also playing a role (Anderson, 2011; Reggente *et al.,* 2016; Watson & Matsuzawa, 2018). Bearzi *et al.* (2017), proposed the 'learning to mother' hypothesis as an explanation, whereby benefits are gained from carrying the corpse of offspring. These useful motor skills can be developed to enhance maternal skills. Carrying a deceased calf is seen to be a direct association of a strong maternal bond in cetaceans, with the mother showing higher levels of attachment due to increased parental investment. It could also be explained by the denial of reality (Bearzi *et al.,* 2017). In humans, following a stillbirth, it is helpful to mitigate separation trauma; the same might be the case in nonhuman species such as cetaceans (Bearzi *et al.,* 2017). However, it is not only mothers who carry the bodies of their deceased offspring. Juvenile female primates have also been observed to carry a dead infant, displaying allomothering behavior (Anderson, 2011; Watson & Matsuzawa, 2018). Whilst it is physically impossible for an elephant mother to carry her infant for long periods of time, reports exist of mothers pushing or kicking their offspring, trying to get them to their feet, or remaining at their side caressing the corpse, long after they had died (Bradshaw, 2004; Moss, 2012).

It is important to note that the research discussed here highlights short-term responses to death regardless of the status of the deceased. The current study aims to understand what happens after these responses. As discussed throughout, because elephants are an extremely complex species, it is logical to assume that there may be longer-lasting changes following the death of a conspecific. Anecdotal evidence from animals often kept as pets, such as dogs, cats and rabbits, has found that that after the death of a companion, animals appear bereaved, often displaying depressive-like symptoms, with symptoms being ameliorated through the introduction of a younger companion whom the grieving animal can nurture (King, 2013). We do not know if elephants, or any nonhuman species, grieve. We risk the issue of anthropmorphising when referring to grief as an emotion in animals, yet, it seems logical to assume that complex, social animals, such as elephants, can grieve, with behavioral and emotional outcomes, including distress, depression and

compulsive behavior, following the loss of a companion (Anderson, 2016; Bearzi, Kerem, Furey, Pitman, Rendell & Reeves, 2018). In elephants, an increase in head-swaying, a known stereotypic, or abnormal behavior, has been associated with separation from conspecifics (Greco, Meehan, Heinsius & Mench, 2017).

It is beyond the scope of this paper to prove, or negate, the possibility of elephants grieving. We will rather provide an overview of behavior and personality in a captive Asian elephant herd, describing how behaviors and personality before death, at a baseline level, differed quantitatively from that after the death of herd members. Most captive herds tend to be small, housing fewer than five individuals, with the majority being unrelated (Rees, 2009). Chester Zoo in the UK provides a rare opportunity to observe a family herd. We measured proximity, using the Hinde and Atkinson Index (1970), alone time duration and affiliative interaction frequencies over three time periods. Personality was also measured, over three time periods, using the Ten-Item Personality Inventory (TIPI) (Gosling, Rentfrow & Swann, 2003). Our analytic focus was primarily exploratory in terms of behavioral and personality changes following the deaths. Overall, we predicted that personality would remain stable over time with the exception of Emotional Stability which we hypothesized would decline following the deaths of herd members as this is the trait most linked to emotional turmoil caused by the death of family members. We also hypothesized that calves would remain in close proximity to their mothers, approximately 70-90% of the time (Lee, 1987; Moss, 2012) and that they would initiate the majority of social interactions.

METHOD

Study Herd & Site

The focal subjects were nine Asian elephants (*Elephas maximus*) housed at Chester Zoo, in the UK (53.2273° N, 2.844° W). The herd comprised one family group, the Hi-Way family, led by matriarch, Thi and her offspring, resulting in a multi-generational herd, presented in Figure 1 below. There were two also unrelated adult elephants in the study herd: a female, Maya, aged 46 and a male, Aung Bo, aged 16, father to all calves.

(Insert Figure 1 – Study herd including the Hi-Way family tree)

Data were collected at three time periods in the current study; all observations were direct. Time 1 (T1) data were collected from December 2017 to April 2018; there were eight elephants under observation during this period. On 17.05.2018, Anjan was born to Thi. On 07.09.2018, Sithami, an integral female within the herd, died suddenly; Time 2 (T2) data were collected after this for a period of four weeks. On 25.10.2018, Nandita and Aayu both died after contracting elephant endotheliotropic herpes virus (EEHV). EEHV was the cause of 53% of deaths in Asian elephants in North America born since 1980 and the cause of 60% of deaths in Asian elephants born since 1995 in Europe making it the biggest cause of death in elephants both in Europe and America (Howard & Shaftenaar, 2019). Time 3 (T3) data were collected following the deaths of Nandita and Aayu. A timeline of events can be seen in Figure 2.

(Insert Figure 2 – Timeline of Events)

The elephants had access to two enclosures, one inside and one outside; there was an accessible pool in the outside enclosure. Adult male, Aung Bo, was periodically removed from the herd at approximately 2pm every day, replicating the natural socialisation patterns of wild male elephants; the male was housed in a separate indoor enclosure parallel to the indoor female enclosure. Upon the zoo opening to the public at 10am, the elephants were moved into the outdoor enclosure, for weather-dependant durations, before returning to the indoor enclosure in the afternoon at approximately 3pm. Observations were conducted in both the outdoor and indoor enclosures. Food was constantly available in the form of baskets of hay as top-feeders. They were provided with additional vegetables

from keepers twice a day. Ethical approval was obtained from the University of Chester School of Psychology Ethics Committee and research approval was given by Chester Zoo.

Material & Measures

A check sheet and ethogram (see Table 1) were was used to record behavior and proximity via all occurrence and instantaneous sampling (Altmann, 1974; Martin & Bateson, 2009). A stopwatch was used during instantaneous sampling.

Proximity was measured using the Hinde and Atkinson Index (1970), the formula for which is presented below (Figure 3). By counting the number of approaches and leaves for each individual within each dyad, the Hinde and Atkinson Index is used to establish which individual within a dyad takes the primary role in maintaining proximity between the two. The resulting figure falls between -1 and +1. A value of -1 indicates that non-focal individual (or B) is solely responsible for proximity; a value of +1 means that the focal individual (or A) is solely responsible for proximity. Scores around zero suggest equal responsibility. Social relationships are argued to be the outcome of a series of interactions within a dyad; individual contributions to the relationship, including maintenance of proximity, are a way of evaluating relationship quality (Silk, Cheney & Seyfarth, 2013; Weaver & de Waal, 2002). The Hinde and Atkinson Index is a systematic method of describing individuals' behavior and their relationships with others, producing a simple numerical value allowing for clear hypothesis testing and comparisons (Silk *et al*., 2013).

(Insert Figure 3 – Hinde and Atkinson Index)

Personality was measured using the Ten-Item Personality Inventory (TIPI) (See Table S1). The TIPI is praised for its simple methodology, comprising of ten brief statements, thus making it quick to

complete by reducing any item redundancy (Gosling *et al.,* 2003). The TIPI is based around the Five-Factor model with each statement corresponding to the relevant trait; Extraversion, Agreeableness, Conscientiousness, Emotional Stability and Openness to Experience. Upon completion, each individual has a score falling between 1 and 7 for each trait. Each trait was defined fully (Gosling & John, 1999; Highfill & Kuczaj, 2007; See Table S2). The primary observer was familiar with the focal elephants potentially raising questions surrounding bias. However, observer ratings are seen as valuable, being the most popular method for assessing personality (Horback *et al.*, 2013; Tetley & O'Hara, 2012). Individuals can, by proxy, accurately and reliably identify discriminant personality traits, useful for long-term behavioral management (Horback *et al.*, 2013).

Procedure

During the non-invasive observations of the Asian elephants, data were collected at three time periods, via all occurrence and instantaneous sampling; a combination of more than one sampling method being deemed most effective (Altmann, 1974; Martin & Bateson, 2009). Each elephant was observed for the same duration during each time period. Focal subjects were observed for fifteen minutes at a time and the following behaviors were recorded:

a) The amount of time individuals spent with each other; this was measured as a percentage of available time in minutes.

b) Approaches and leaves to determine which individuals were more responsible for initiating proximity. This was measured using the Hinde and Atkinson Index (1970). Proximity was defined as

a trunk's length distance under the premise that, if they wanted, an individual could touch those proximal to them. Elephants of different ages would have varying trunk lengths, therefore the definition of a 'trunks length' was operationalised as much as possible with the primary researcher making the final ruling.

c) Durations of behaviors. Behaviors were grouped into two sub-categories: Social and Alone behavior; see Table 1 for definitions.

d) The frequency of affiliative interactions (see Table 1 for definitions). The direction of interaction within a dyad was also recorded.

e) Personality was measured using the TIPI (Gosling *et al*., 2003) at the end of each time period to establish changes over time. Inter-rater reliability was also obtained.

(Insert Table 1 here – Ethogram of behavior)

Design & Analysis

The current study was purely observational. Behavioral analysis was conducted first on a herd level, whereby the elephants were split into two categories – Adult Elephants and Infant Elephants – based upon age. Elephants aged eleven-years and older were categorised as Adults, those younger (newborn to ten years old) were referred to as calves and categorised as Infant elephants (Moss, 2012).

The Adult elephants were Maya, Thi, Aung Bo, Sithami and Sundara, the Infant elephants were Nandita, Indali, Aayu and Anjan, creating a near equal divide of the study herd. Tests of normality were not performed due to small sample size and the mean was chosen over median as in such samples, values are typically similar yet the mean is argued to potentially give a more accurate representation of frequencies and durations of behavior (Martin & Bateson, 2009). Analysis was also

conducted on an individual level for each of the herd members separately, assessing behaviors on a dyadic level. Reliability analysis was conducted as a percentage agreement for the TIPI. Spearman's correlation analyses were conducted, using SPSS Software, on data from T1, T2 and T3 to assess relationships within and between behaviors, individual age in years and personality traits across time; the alpha level was set at .05.

RESULTS

Proximity and behavior were first assessed on a herd level; the herd was split into two categories Adult Elephants and Infant Elephants. Means of the elephants' Hinde & Atkinson proximity scores, Affiliative Interactions, Association durations and Alone Time durations are presented in Table 2. Individual scores of these components are presented as Appendices: Table S3: Individual Hinde & Atkinson Scores across T1, T2 and T3; Table S4 Individuals' Alone Time Mean across T1, T2 and T3. Table S5: Individuals' Association Patterns across T1, T2 and T3 and Table S6: Shared Affiliative Interactions across T1, T2 and T3.

Herd-level analysis

(Insert Table 2 here - Mean Scores of Adult and Infant elephants).

Infant elephants initiated the majority of Affiliative Interactions on average; Affiliative Interactions at T2 were negatively correlated with Age ($r(8)= -.731$, $p=.040$). Adult Elephants consistently spent more time alone; Age was positively correlated with Alone Behaviors at T2 ($r(8)=.810$, $p=.015$) and

negatively correlated with Social Behaviors, and therefore, negatively correlated with the time spent with others, at T2 ($r(8)=-.857$, $p=.007$). Further correlations are presented in Table 3.

(Insert Table 3 here – Correlation matrix of Personality and Behavior).

Although the TIPI has not been used to assess personality in elephants prior to this, we found 95% agreement between raters; it was seen to provide an accurate reflection of the individual personalities observed. We did not calculate the Cronbach's alpha for internal scale reliability due to each trait only having two items. Most personality traits remained stable over time with positive correlations observed across time for Agreeableness (T1 to T2; T2 to T3), Conscientiousness (T1 to T2; T1 to T3), Emotional Stability (T2 to T3) and Openness to Experience (T1 to T2; T2 to T3). Individual personality scores can be found in Table S7. The personality traits Conscientiousness and Emotional stability (both higher in Adult Elephants) and Openness to Experience (higher in Infant Elephants) were regarded as age-related traits; correlations between age and the aforementioned traits are presented in Table 3. The traits deemed "Adult Traits" (Conscientiousness and Emotional Stability, with the addition of Agreeableness) positively correlated with one another consistently over time.

Hinde and Atkinson Scores at T1 negatively correlated with Emotional Stability at T1 ($r(8)= -.912$, $p=.002$) and T2 ($r(7)=-.906$, $p=.005$). During T1, the individuals with the most positive, and thus highest, Hinde and Atkinson mean score were adult male, Aung Bo and infant male, Aayu; both of these individuals scored relatively low in Emotional Stability hence explaining the relationship between these two variables.

Individual-level analysis

Maya. Maya's Hinde and Atkinson value was relatively close to zero consistently, across the three time periods, but a negative score indicates that other elephants maintained proximity more with her. In T1, she spent the largest amount of time with Aayu, followed by Thi and then Nandita. She directed the most affiliative interactions towards calves Aayu, Nandita and Indali. In T2, the amount of time Maya spent on average with others decreased from 17.7% in T1 to 5.6% in T2. Corresponding with this, the amount of time she spent alone doubled. During T3, after the loss of Maya's two most frequent associates, Nandita and Aayu, her time spent with Thi increased as did that with Anjan and Indali. Indali was the recipient of the most affiliative interactions, resulting in Maya spending markedly less time alone.

Maya's personality scores remained largely consistent across time. A change in Agreeableness was observed; it decreased from 6.0 in T1 to 5.5 in T3, coinciding with anecdotal observations of Maya directing agonistic behavior to calf Indali, kicking her and pulling her trunk. Maya decreased in Emotional Stability after the deaths (in T2 and T3).

Thi. The Hinde and Atkinson Index value of Thi remained largely stable over time, with a negative score indicating that she did not take responsibility for maintenance or changes in proximity. In T1, Thi spent a large amount of time with her adult and younger offspring, Sithami and Nandita respectively, as well as grandson, Aayu. She also spent a large amount of time with Maya, with whom she has a close relationship, despite being unrelated. The affiliative interactions Thi initiated towards daughters Sithami and Nandita were equal, despite the difference in age; she directed the most affiliative behaviors towards grandson Aayu. In T2, she spent notably less time with Maya, but more time with Nandita. She also spent 29% of her available time with newborn calf, Anjan, which is to be expected. In T3 she spent more time with Maya and less time alone.

Thi scored high in adult traits Conscientiousness and Agreeableness; these remained consistent over time. Her Emotional Stability scores increased from 4.0 in T1 to 5.5 in T3.

Aung Bo. Aung Bo was the elephant with the most consistently positive Hinde and Atkinson Index value across the three time periods; approaching others more frequently and leaving less. He still spent a large amount of time alone (T1 – 85%; T2 – 76.2%; T3 – 79%). When socialising in T1 and T2, he spent the majority of time with calves, Nandita and Aayu, yet continuously directed the most affiliative interactions towards Maya. During T3, Aung Bo's time spent with others increased to 8.3% on average, spending more time with Thi, Sundara, Indali and Anjan, although still spending a large amount of time alone.

Aung Bo's Extraversion and Openness to Experience scores increased in T2 and T3.

Sithami. Sithami's Hinde and Atkinson Index score was -0.05. Although close to zero, the negative value indicated that the other elephants were more responsible for maintaining proximity within the dyad. She spent most of her time with her calf, Aayu, reinforcing the close bond between mother and calf. Sithami spent the second largest amount of time with younger sister, Nandita, followed by mother Thi, to whom she directed the greatest amount of affiliative interactions.

Sundara. Sundara's Hinde and Atkinson Index mean score declined from a low positive value in T1 to an increasingly negative value in T2 and T3 meaning that she was less responsible for maintaining proximity with others at this time, suggesting that other individuals approached her more frequently. Yet, the average approaches received decreased from 24.7 in T1 to 13.4 in T2 and 8.4 in T3, suggesting that the decline was attributable to other factors, such as others leaving less frequently.

During T1, Sundara spent the largest amount of time with daughter, Indali, followed by younger brother, Aayu. She directed most affiliative interactions towards Nandita, Indali and Aayu. During T2, she spent less time socialising with others; her affiliative behaviors decreased when directed to daughter, Indali, but increased towards brother Aayu. During T3, the time Sundara spent with the

other elephants, overall, increased to 13% on average, including time spent with male, Aung Bo, and infants, Indali and Anjan.

Sundara's Extraversion scores in T2 and T3 increased and she was observed engaging with the infants and exhibiting play behavior. Her Openness to Experience score also increased in T2.

Nandita. Nandita's Hinde and Atkinson Index mean score did not change meaningfully, remaining relatively close to zero in both T1 and T2. During T1, Nandita's closest associates were her age-related peers, Indali and Aayu, with whom she spent a large amount of time engaging in play behaviors. She also spent a large amount of time with mother, Thi. In T2, she spent more time alone.

Nandita's Agreeableness score, however, increased by more than double from 2.0 in T1 to 4.5 in T2 and she was observed to display allomaternal behaviors, directed towards younger brother Anjan. Similarly, Nandita's Emotional Stability increased from 4.0 in T1 to 5.5 in T2.

Indali. Indali's Hinde and Atkinson Index mean score remained largely consistent over the three time periods, suggesting stability over time. During T1, Indali spent the largest amount of time with playmates, Nandita and Aayu, directing the most affiliative contacts towards Aayu. In T2, however, the time spent with Nandita and Aayu decreased; Indali opted rather to spend more time with Anjan. In T3, following the deaths of Nandita and Aayu, the affiliative interactions she directed towards Anjan increased dramatically. Indali also spent more time with Aung Bo, approaching him more frequently during T3 (8.0) than T1 (5.0) and T2 (4.0).

Indali decreased in Emotional Stability after the deaths, supporting the original hypothesis. Indali also became more Extravert and Open to Experiences in T3.

Aayu. The Hinde and Atkinson Index values for Aayu were closer to zero across the two time periods. In T1, Aayu spent the majority of time with Nandita, followed by mother, Sithami, spending the largest amount of time with his mother (36%) than other calves did with their respective mothers. The time Aayu spent with the other elephants changed following the death of his mother, Sithami. Most notably, the amount of time he spent alone increased vastly. This resulted in a decreased amount of time spent with Nandita and Aayu. In T2 he spent the largest amount of time with Anjan, directing the most affiliative interactions towards him. In T2, his Agreeableness, Extraversion and Emotional Stability scores also decreased.

Anjan. Anjan's Hinde and Atkinson mean score increased from T2 to T3. The amount of time he spent with his mother Thi decreased in T3. In T3, the time Anjan spent with Maya, Aung Bo and Sundara increased, as did Anjan's time with Indali, including increased affiliative interactions directed towards her.

His personality scores remained largely consistent, with the only change being visible in his Openness to Experience score as he became more confident to go further alone.

DISCUSSION

The current study explored changes in personality and/or behavior in response to the death of herd members. It posed the question whether these responses would differ based upon the status of the deceased or due to the relationship between deceased and survivor.

How does the death of an adult female affect her infant calf?

Changes in both personality and behavior were observed in an infant male, Aayu, whose mother died when he was just eighteen-months-old. In comparison with the other calves and their respective mothers Aayu was the infant who spent the most amount of time with his mother, on average (36%) – Nandita spent 30.5%, on average, of her available time with her mother; Indali 20.6% on average and Anjan 25% on average (See Table S5 for individual dyadic scores). This was, however, less than what was initially predicted (70-90%), not supporting the original hypothesis (Lee, 1987; Moss, 2012; Petraccione *et al.*, 2017). Following his mother's death, data from T2 indicated that the amount of time he spent socialising with other members of the herd decreased, resulting in an increased amount of time spent alone. We know that maturational changes in behavior, such as an increase in solitary behavior, is to be expected in juvenile males, representative of their behavior in the wild (Horback *et al*., 2013; Chiyo *et al*., 2011). This is usually a gradual process, though, with juvenile males spending more time socialising with unrelated adult males, outside of their natal herd; recreating such settings in a captive environment remain difficult (Hartley *et al*., 2019). Yet, at such a young age, these changes were unexpected so, therefore, cannot be attributed to maturation, but rather to the death of his mother and thus the impact of maternal deprivation. Personality wise, Aayu was less Emotionally Stable, supporting the initial hypothesis, less Extraverted and less Agreeable, and displayed fewer playful behaviors following the death of his mother. These changes could be likened to the depressive state described by Anderson (2011) in a young male chimpanzee, upon being orphaned. The individual with whom Aayu spent the most amount of time with, and directed the most affiliative interactions towards, was young infant, Anjan, perhaps acting in a nurturing way, supporting previous research that the presence of a younger conspecific to care for can mitigate the effects of loss (King, 2013).

Aayu attempted to suckle both of the remaining lactating females in the herd (grandmother, Thi, and older sister, Sundara); however, none of these attempts were successful and he was pushed away, each time. Whilst there is conflicting opinion surrounding allomothers allowing non-offspring calves to suckle most agree that it makes little sense for an allomother to allow it (Douglas-Hamilton *et al*, 2006; Gadgil & Nair, 1984; Lee, 1987; Vidya, 2014), because it would interfere with the female's care for her own calf, resulting in potentially detrimental effects (Rapaport & Haight, 1987). Following the death of its mother, an infant's risk of mortality increases, even more so when the infant is male (Lahdenepera, Mar & Lummaa, 2016a). Aayu died seven weeks after the death of his mother but it is beyond the scope of this paper to speculate direct causation.

How does the death of an adult female affect the rest of the herd?

The death of Sithami, a highly central adult female, affected the overall herd dynamic, aside from just her dependent offspring, supporting previous research from Gartland *et al*. (2018). We also observed changes of a differing nature in the behavior of Sundara, Sithami's eldest offspring, suggesting that the age of offspring is a variable in determining responses to a mother passing. After the death of her mother, Sundara, who had previously remained on the periphery of the herd, took a more central role, spending more time with the calves and also directing more affiliative behaviors towards younger brother, Aayu. It is known that elephants reassure each other in an affiliative context after a distressing event (Plotnik & de Waal, 2014), due to their intensely social nature and high encephalisation, which via self-regulation and perspective-taking, enables them to display empathic concern for others (de Waal & Preston, 2017).

Nandita, younger sister of deceased Sithami, spent more time alone following her sister's death. This could be attributed to maturation, less dependence on a mother-figure and more confidence to explore

alone; alternatively, it could be due to the loss of Sithami. In the wild, daughters remain with their natal herd across their lifespan; females aid their mothers in caring for younger siblings (Lee, 1987; Moss, 2012). Sithami assumed an allomothering role for Nandita in T1, so the loss of such a close attachment figure would have lasting effects for Nandita. Nandita in turn was observed engaging in allomaternal behaviors directed towards younger brother, Anjan. She was observed engaging in 'collective protection', alongside her mother, Thi, and would circle Anjan, upon approach of adult male, Aung Bo, whom Anjan initially appeared intimidated by (Gadgil & Nair, 1984). Such observations reinforce the notion that allomothering still remains present in captivity, being regarded as an aid for strengthening social relationships and reducing aggression (Schulte, 2000).

The most central female within the herd was matriarch, Thi. During T1, Thi, Sithami and Maya spent a large proportion of time with one another. Sithami was Thi's oldest daughter; Maya had been housed in Chester Zoo with Thi since the early 1990s. The association between Thi and Maya was perceived as close, by the primary researcher, despite being unrelated. Previous research examining social behavior in captive elephants found the strongest association, second only behind the relationship between a mother and her calf, to be between the two oldest females who were unrelated (Petraccione *et al.,* 2017). In T2, following the death of Sithami, the amount of time Thi spent with Maya decreased, and she instead spent understandably more time with her four-month-old calf, Anjan. As a result of her calf's care requirements, she also spent less time with grandson, Aayu. One might have assumed that Thi would wish to spend more time with Aayu, following the death of his mother, providing comfort, due to the perceived close-knit nature of elephant herds, with the presence of a grandmother observed to reduce calf mortality (Lahdenpera *et al.,* 2016b). Thi was more Emotionally Stable in T2 (and T3), which is unexpected, contradicting the original hypothesis that there would be a decline in Emotional Stability following the deaths of herd members. Again, however, this could be explained by the presence of calf Anjan; the same was observed for allomother, Nandita.

Overall, however, following the death of Sithami, both Adult and Infant elephants spent more time alone with an observed decrease in affiliative behaviors. Whilst no direct predictions were made concerning association and affiliative patterns, these findings still remain unexpected given the intensely social context in which we view elephants.

How does the death of two calves affect the herd?

The importance of a calf in a herd is continually emphasised, therefore it is logical to assume that the death of a calf would have a dramatic impact on the surviving herd members. An over-arching increase in individuals' time spent socialising with others was observed, as well as clear changes in personality. For example, the Emotional Stability trait score of the oldest observed female, Maya, declined, as did that of Indali, former age-related playmate of the deceased. Thi spent more time with Maya, her long-term close associate, following the deaths of Nandita and Aayu, potentially seeking comfort. Indali spent more time with her only remaining age-related conspecific, Anjan. Whilst one would assume that the only two remaining infants would spend more time together due to a lack of alternative associates, it is important to stress that prior to the calves' deaths, Indali was not a particularly playful individual (Figures can be seen in Table S7). A potential explanation for this change could be due to increasing demand from Anjan to engage in social activities, resulting in the observed increase in Extraverted behavior in order to fully meet and stimulate his needs. It could also be seen as a method used by Indali to mitigate the effects of her grief, like that observed with Aayu during T2, by nurturing and spending more time with a younger conspecific (King, 2013).

General discussion

The main justification for the current study was to investigate changes in response to the death of herd members, potentially leading to questions regarding the concept of elephant grief. Previous research studying elephants' response to death states that elephants have an interest in the carcasses and bones of conspecifics (Douglas-Hamilton *et al.*, 2006; McComb *et al*., 2005). Research from Sharma *et al.* (2019) states that Asian elephants may feel distress following the death of a conspecific, but this study discusses only short-term behaviors observed, including exploratory and epimeletic behaviors, without any assessment of long-term behavioral or psychological changes in surviving individuals. Our study has documented clear changes in both behavioral patterns and personality traits following two major alterations to the herd.

We observed, as predicted, changes in Emotional Stability. These changes, however, were reliant upon who died and the presence of dependent offspring. For example, following the death of Sithami, Thi's Emotional Stability increased due to the presence of her young calf who was utterly reliant upon her, but decreased in Sithami's orphan, Aayu. Following the deaths of Nandita and Aayu, Emotional Stability remained consistent in Thi, a mother with a dependent calf, but declined in those without dependent offspring regardless of age – changes were observed in the oldest female and in a two-year-old female. This clearly highlights the importance of context, suggesting that the presence of a calf is a mediating factor and that potentially, without the presence of a new calf to care for, results may have been different.

Who died was important. It allowed for an important differentiation between responses, not all of which conformed to previous research. The herd spent more time alone following the death of an adult female but more time together, including an increase in affiliative interactions towards one another, after the death of two calves. This suggests that a calf's death affects and ultimately changes the behavior and personality of remaining herd members more severely than the death of an adult

female. These changes are however, dependent upon the strength of relationships to the deceased – the most dramatic change was observed in an orphaned calf who had lost its mother. This was also mediated by age. Sithami was survived by two offspring, her dependent, infant offspring, Aayu, became more solitary and increasingly depressed whereas her older, independent daughter, Sundara, with a daughter of her own, assumed a more central role within the herd.

A further behavior of interest, although not initially reported, was head swaying, particularly common in matriarch, Thi; head swaying is regarded as a stereotypic behavior linked to separation from conspecifics (Greco *et al.* 2007). Whilst Thi exhibited head swaying before, it was anecdotally observed to be more prevalent in T2 and T3, following the deaths of Sithami, Nandita and Aayu, therefore, offering support for Greco *et al.'s* (2017) suggestion that it can be exacerbated by the death of a companion. It is recommended that future studies include head-swaying as an observed behavior to assess this concept quantitatively.

Our study is pioneering in its use of the TIPI to measure personality in elephants in contrast to the more extensive, inductive personality measures (Lee & Moss, 2012; Seltmann *et al.,* 2018). The TIPI, whilst initially created for assessing personality in human subjects, is a quick and easy measure, requiring no statistical knowledge. This is of particular importance as this method could be employed regularly and efficiently by keepers to assess personality and highlight implications for wellbeing in captive elephants at particular times including unusual situations such as herd alterations resulting from births or deaths. Overall, through its ability to measure consistency in traits across time, we found the TIPI to be applicable to elephant personality. The TIPI has, however, been criticized for limiting personality to just five traits (McAdams, 1992). Furthermore, the TIPI could be deemed too anthropomorphic, possessing adjectives initially targeted towards a human subject, therefore, seemingly inappropriate for the study personality in a nonhuman species. It is recommended for

further research to employ the use of an animal-specific personality measure, alongside the TIPI, to assess stability across measures.

To conclude, we found evidence of change in both personality and behavioral patterns following the death of herd members. Responses differed based upon who died and the strength of relationships held. But, how closely do these changes resemble what one might refer to as grief? While there is the risk of anthropomorphising when referring to grief as an emotion held in animals, we still need to remain careful not to negate the ability of elephants to grieve based solely upon their inability to communicate. It is beyond the scope of this paper to speculate as to the existence of grief, but what we can say with certainty is that the death of herd members produces obvious change.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

Contributors:

LR and LM designed the study, LR collected the data, LR and LM analysed the data, wrote and approved the paper. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for profit sectors.

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TABLES

Table 1 Ethogram of behavior

Behavior	Operational Definition
Proximity	Another elephant is within a trunk's length from the focal elephant.
Affiliative Behavior	Involving the touching of another with trunk or body, usually around the individual's face, trunk, mouth, chest or back. All affiliative behaviors were coded the same for the current study.
Affiliative Interactions	A dyad are exhibiting affiliative behaviors; affiliative behaviors include contact rubbing or trunk-to behaviors.
Alone Behaviors	Engaging in any of the following behaviors whilst alone. No other elephants are within a trunk's length of the focal individual.

	Eating Alone	Reaching for food with one's trunk and eating. It is counted as continuous eating even if reaching up for food more than once.
	Exploring Alone	Including walking from one side of the enclosure to the other.
	Just Alone	Elephant is not exhibiting any observed behaviors.
	Play Alone	Sand play, object play and water play.
Social Behaviors		Engaging in any of the following behaviors whilst proximal to others. Other elephants are within a trunk's length of the focal individual.
	Eating with Others	Including the process of reaching for food with one's trunk as well as the process of eating itself. It is counted as continuous eating even if reaching up for food more than once.
	Exploring with Others	Walking from one side of the enclosure to the other.
	Just with Others	Elephant is not exhibiting any of the above behaviors.
	Play with Others	Play fighting, sand play and water play.

Table 2 Mean Scores and (Standard Deviations) of Adult and Infant elephants

	Adults			Infants		
	T1	T2	T3	T1	T2	T3
Hinde & Atkinson Index	0.01 **(0.02)**	-0.03 **(0.17)**	-0.02 **(0.15)**	0.00 **(0.52)**	-0.02 **(0.11)**	0.03 **(0.43)**
Affiliative Interaction Frequency	02.4 **(01.2)**	01.9 **(00.4)**	02.3 **(00.9)**	10.0 **(02.6)**	08.6 **(02.5)**	13.4 **(01.0)**
Association Duration	14.2 **(06.9)**	07.1 **(05.2)**	16.4 **(07.0)**	26.5 **(04.6)**	16.6 **(01.9)**	20.3 **(00.8)**
Alone Duration	49.2 **(23.1)**	64.6 **(11.5)**	48.5 **(27.4)**	14.0 **(01.0)**	25.0 **(13.4)**	28.8 **(17.3)**

Note. *Hinde & Atkinson Index expressed as a mean score; Affiliative Interaction Frequency expressed as mean rate per hour; Durations expressed as percentage of available time in minutes

Table 3 Correlation matrix of Personality, Age (in years) and Behavior

Age	H1	H2	H3	E1	E2	E3	A1	A2	A3	C1	C2	C3	ES1	ES2	ES3	O1	O2	O3
Age	-.443 .272 8	.381 .353 8 .234 613 7	-.200 .704 6 .400 .505 5 .600 .208 6	-.466 .244 8 -.259 .535 8 .200 .667 7 .105 .866 5	-.268 .520 8 056 .905 7 .390 .339 8 **.841*** .036 6 .415 .354 7	-.667 .148 6 -.154 .805 5 .058 .913 6 .522 .288 6 .676 .210 5 .574 .234 6	.381 .352 8 -.346 .401 8 .055 .908 7 -.316 .604 5 .070 .870 8 -.359 .430 7 -.487 .406 5	.554 .154 8 -.587 .166 7 -.217 .606 8 -.551 .257 6 -.287 .535 7 -.617 .103 8 -.632 .178 6 **.833*** .020 7	.677 .140 6 -.616 .269 5 -.029 .956 6 -.530 .280 6 .189 .760 5 -.478 .338 6 -.702 .120 6 **.973**** .005 5 **.985**** .000 6	**.835**** .010 8 -.550 .158 8 -.036 .938 6 -.410 .493 5 -.494 .214 8 -.472 .285 7 -.658 .227 5 -.557 .152 8 **.870*** .011 7 **.947*** .014 5	**.810*** .015 8 -.559 .192 7 -.119 .779 7 -.543 .266 6 -.527 .224 7 -.586 .127 8 **-.814*** .036 6 .618 .139 7 **.904**** .002 8 **.971**** .001 6 **.927**** .003 7	.771 .072 6 -.500 .391 5 .029 .957 8 -.543 .266 6 .000 1.00 5 -.522 .288 6 **-.841*** .036 6 **.949*** .014 5 **.928**** .008 6 **.971**** .001 6 **.975**** .995 5 1.00 - 6	.342 .406 8 **-.912**** .002 8 -.217 .641 6 -.564 322 5 .286 .521 8 -.409 .362 7 158 800 5 .504 .203 8 .632 .128 7 .500 .391 5 .589 .125 8 473 .284 7 410 .493 5	**.717*** .046 8 **-.906**** .005 7 .012 .977 7 -.441 .381 6 .020 .984 7 -.241 .566 8 -.388 .447 6 .372 .412 7 .675 .066 8 .803 .054 6 .572 .180 7 **.791*** .019 8 .765 .076 6 .692 .085 7	**.880*** .021 6 -.447 .450 5 .334 .518 8 -.273 .600 6 .177 .776 5 -.308 .553 6 -.739 .093 6 **.884*** .047 5 **.882*** .040 6 **.907*** .013 6 .860 .061 5 **.941**** .005 6 **.941**** .005 6 .287 .640 5 **.813*** .049 6	-.494 .213 8 -.285 .494 8 -.036 .939 6 .205 .741 5 **.926**** .001 8 .449 .321 7 .533 .334 5 -.037 .930 8 -.183 .694 7 .368 .542 5 -.472 .238 8 -.378 .403 7 .154 .805 5 .199 .637 8 .132 .778 7 .287 .640 5	**-.751*** .032 8 .009 .984 7 -.200 .636 7 .525 .285 6 .734 .061 7 .513 .194 8 **.939**** .005 6 -.543 .208 7 -.583 .130 8 -.699 .122 6 **-.886**** .008 7 -.701 .053 8 **-.833*** .039 6 -.134 .774 7 -.286 .493 8 -.754 .083 6 **.812*** .027 7	-.657 .156 6 .000 1.00 5 .086 .872 8 .714 .111 6 .527 .361 5 .638 .173 6 **.899*** .015 6 -.369 .541 5 -.493 .321 6 -.599 .249 6 -.564 .322 5 -.714 .111 6 -.714 .111 6 -.103 .870 5 -.412 .417 6 -.577 .231 6 .667 .219 5 **.926**** .008 6
H1																		
H2																		
H3																		
E1																		
E2																		
E3																		
A1																		
A2.																		
A3																		
C1																		
C2																		
C3																		
ES1 .																		
ES2																		
ES3																		
O1																		
O2																		

Order of values presented above: Spearman Correlation, Significance (2-tailed), N (Sample Size). Variables: Age (Age); H1 (Hinde & Atkinson Mean T1); H2 (Hinde & Atkinson Mean T2); H3 (Hinde & Atkinson Mean T3); E1 (Extraversion T1); E2 (Extraversion T2); E3 (Extraversion T3); A1 (Agreeableness T1); A2 (Agreeableness T2); A3 (Agreeableness T3); C1 (Conscientiousness T1); C2 (Conscientiousness T2); C3 (Conscientiousness T3); ES1 (Emotional Stability T1); ES2 (Emotional Stability T2); ES3 (Emotional Stability T3); O1 (Openness T1); O2 (Openness T2); O3 (Openness T3.
Coefficients in red are significant (**p*<.05 / ** *p*<.01).

FIGURES

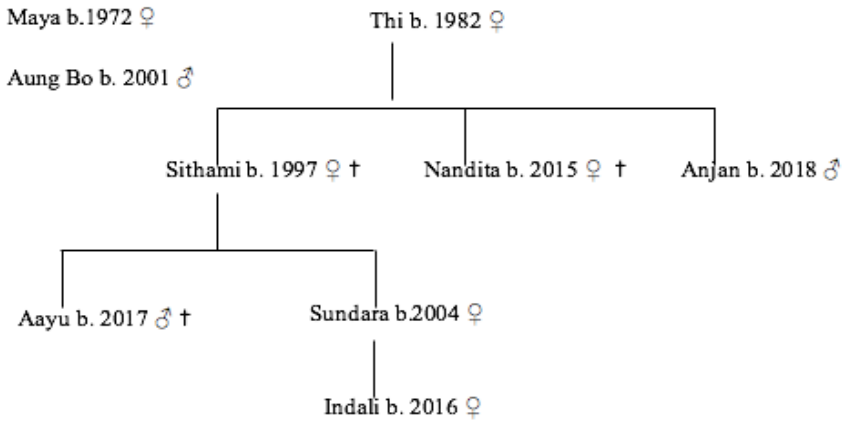

Figure 1 Study herd at Chester Zoo including the Hi-Way family tree.

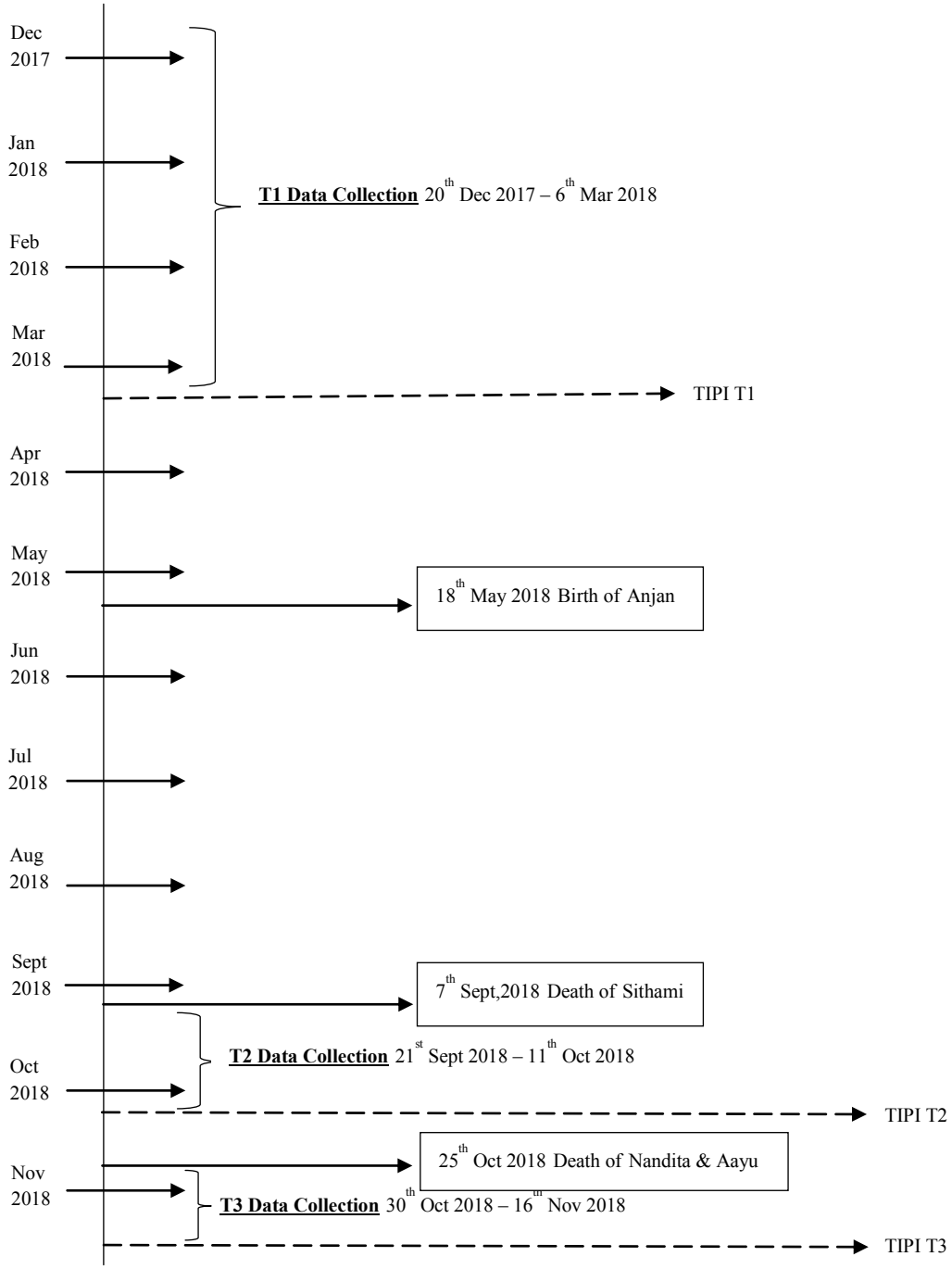

Figure 2 Timeline of Events.

$$\frac{\text{A approaches B}}{\text{(A approaches B + B approaches A)}} - \frac{\text{A leaves B}}{\text{(A leaves B + B leaves A)}}$$

Figure 3 Hinde and Atkinson Index.

Note. A value of -1 indicates that non-focal individual (or B) is solely responsible for proximity; a value of +1 means that the focal individual (or A) is solely responsible for proximity; scores around zero suggest equal responsibility.

Within a captive herd of Asian elephants (Elephas maximus) housed at Chester Zoo, UK, we measured social behaviour, proximity and personality and found age-related and relationship-related changes in both behavior and personality following the deaths of herd members. We found a greater impact on the behaviour and personality of surviving herd members following the deaths of calves, compared to an adult member, which attests to the significance of a calf's unifying role within an elephant herd.