The effect of friendships on the health of the Asian elephant

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Master's thesis
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Faculty of science and engineering
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18.4.2019

Ecology and evolutionary biology
40 ects

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TUOMISTO, MATLEENA: The effect of friendshpis on the health of the Asian elephant

Master's thesis, 26 p., 2 appendices, total 44 p.
Ecology and evolutionary biology
April 2019

Abstract

The link between health and social relationships has been extensively studied in humans, but significantly less in other species. Here I study another large, social and long-lived mammal species, the Asian elephant (*Elephas maximus*), to determine whether friendships affect their health. The study population is a semi-captive population working in the timber industry in Myanmar. The semi-captivity of the population offers a unique chance to obtain extensive and accurate data from a population resembling a wild population significantly more than one in a zoo. Sixteen health-related variables were measured, and linear models were run for each to determine whether having friends affects these. I found that cortisol levels are higher in solitary individuals, and there were higher levels of protein in the blood of solitary males than males with friends. I also found that individuals with relatives as friends were less likely to have trematode parasites, were heavier, had lower systolic blood pressure and higher cortisol than those who didn't have relatives as friends. A majority of relative-friends are the focal elephant's own baby, which offers an explanation for differences in mass and cortisol. Solitary individuals having higher cortisol levels is consistent with research done on other social species. Total protein can indicate multiple things, thus the reason for and implication of differing levels is currently unknown. This study suggests that friendships have some effect on elephants' health, which could have implications for captive management and conservation. More research is required to determine the effects more accurately.

Keywords: Elephant, *Elephas maximus*, sociality, friendships, health

Contents

1. Introduction

Social relationships between individuals has been a topic of interest for research for decades. In the 1960's it was suggested that sociality has evolved as a way of increasing an individual's inclusive fitness through kin selection (Hamilton 1964). While kinship is probably one reason for an animal to be social, friendships are formed also between non-kin individuals. In many species the social bonds, both with kin or non-kin, can increase an individual's direct fitness, increasing both survival and reproduction (Seyfarth & Cheney 2012) In general, sociality evolves when the benefits of cooperation, such as defence against predators or more efficient hunting, exceed the costs of living close to other individuals, such as resource competition and transmission of infectious diseases (Silk 2014).

The relationships that individuals of social species form can often be close and long-lasting, very much akin to human friendships. Despite this, some researchers have been hesitant to call these relationships friendships and argue that calling them friendships is anthropomorphism. When studying humans, defining friends and friendships is easy: a person's friends are those people they feel are their friends. When studying animals, the study subjects cannot simply be asked who they see as their friends or how close they are to them. However, it is not far-fetched to speak of friendships in the case of a species such as non-human apes, dolphins or elephants that form relationships that last for years or decades and seem, to an outside observer, affectionate and close. (Moss et al. 2011; Seyfarth & Cheney 2012)

Social relationships in non-human species have been studied from multiple points of views. Social network structures, or with whom the individuals are friends, have been studied for example in chimpanzees (*Pan troglotydes*) and baboons (*Papio cynocephalus*) as well as in fish (guppies, *Poecilia reticulata*, and three-spined sticklebacks, *Gasterosteus aculeatus*) (Croft et al. 2005; Massen & Koski 2014; Silk et al. 2006). Especially females in many species often associate with matrilineal kin, but close friendships are also formed between non-kin individuals who are similar in social rank or age (Seyfarth & Cheney, 2012). Having close relationships has been linked to longevity in baboons (Silk et al. 2010). The effects of social relationships on reproductive success has also been studied in some species, such as feral horses (*Equus ferus caballus*) and prairie voles (*Microtus ochrogaster*). Horses live and reproduce in non-kin groups, and females had a higher reproductive success if they

were well integrated into their group (Cameron et al. 2009). Prairie voles had the highest reproductive success when they lived in groups of three adults (McGuire et al. 2002).

Health is an equally complex issue as social relationships. Sartorius (2006) identified three different ways of defining health: as lack of disease, as a state that allows an individual to adequately cope with daily life, and as an equilibrium both within an individual and between individual and its surroundings. Health is thus a much more complex issue than simply an absence of disease, and the metrics used are more complex than simply the presence or absence of disease. The ability to adequately cope with daily life can be hindered by physical disease, but also by mental health problems or stress. By equilibrium Sartorius refers to a state where, despite possible illness, the individual is able to live life as well as possible. However, equilibrium could also be interpreted as a state where the body functions remain at a level that enables the individual to be and remain healthy based on the other two definitions. This kind of health can be assessed by measuring those functions of the body.

Of these measures of health, the effects of social relationships on stress have been studied in multiple species. It is a long-known fact that social isolation is a stressor for social animals (Hatch et al. 1965), and stress caused by social isolation has been found to delay wound healing in Siberian hamsters (*Phodopus sungorus*) (Detillion et al. 2004). Others have studied social buffering, which refers to the faster recovery from stressful situations if there are other individuals around to help (Kikusui et al. 2006). Furthermore, it has been shown that social structure affects stress hormone levels of individuals at different positions in the hierarchy (Creel 2001); and how change in social structure affects stress hormone levels (Beehner et al. 2005; Bergman et al. 2005).

Other studies on sociality and health have found, for example, that in rats, social isolation triggers higher food consumption and results in an increase in body weight (Jahng et al. 2012). Close associations between individuals increases the probability of parasite transmission and thus the parasite load of individuals (Arneberg et al. 1998), although other studies have not found a similar difference (for example Vuren 1996). In humans, loneliness has also been found to increase blood pressure, which increases the risk of cardiovascular problems (Shankar et al. 2011).

In elephants, sociality has been extensively studied especially in a population of African savanna elephants (*Loxodonta africana*) living in the Amboseli national park, where the

world's longest study on these animals has been conducted since 1972 (Moss et al. 2011). These elephants have been studied for decades to identify the social structure of the population and the changes occuring in it. The females spend their time in groups that consist of close kin. The groups are led by the oldest female and the rest of the individuals are typically her daughters and granddaughters. Males spend their youth in the female groups with their mothers, but leave the group and disperse at 9-15 years of age, usually in degrees over many years. The family groups can also temporarily split up into smaller groups, but they always come back to the family group. The family groups can also temporarily join together with other families to form a larger group. Often the family groups that join together consist of individuals that are kin, though farther kin than the individuals in each family group. However, even though the elephants associate most often with kin, they do not exclude non-kin. Also unrelated females are accepted into groups and treated in the same way as the others in the group. (Moss et al. 2011)

Male elephants don't form similar permanent groups as females, but also spend time in groups. Especially younger males (who have already left their natal family) spend some of their time in mixed male-female groups. Males also form all-male groups. The time spent in any kind of group decreases with age: the oldest males spend the highest proportion of their time alone. The time spent alone or in groups varies highly between males, as does how selective they are about with who they spend their time when they are not alone. Some males associate evenly with a lot of other individuals whereas others prefer to spend their time with some particular individuals. (Moss et al. 2011)

It is not entirely clear, however, how much of our knowledge about the social structure of African savanna elephant applies to Asian elephants (*Elephas maximus*). Asian elephants' social structures have been studied less than those of African elephants, probably due to the fact that it is easier to observe and follow animals on a savanna than in a forest, the Asian elephants' natural habitat. Like African savanna elephants, Asian elephants have been found to have a matriarchal structure: the groups they commonly spend time in are matrilineal kin, though the family groups are smaller than those of African savanna elephants and typically only consist of 2-3 adult females and possible calves (Fernando & Lande 2000; Vidya & Sukumar 2005). The ties between individuals are on average weaker than between African savanna elephants, although most individuals have also a few strong ties to others, as well as long-lasting ties. While each elephant spends time with varying individuals, a larger social network of individuals stays relatively stable over time (de Silva et al. 2011).

Despite a large number of studies on both health and friendships, the vast majority of more extensive studies on the relationship between the two has been done in humans. In humans, social relationships and friendships have been connected to health factors from mental health to mortality (Holt-Lunstad et al. 2010), and loneliness has been found to increase disease risk for for example coronary heart disease and stroke (Valtorta et al. 2016) and dementia (Holwerda et al. 2014). Since most of what we know about friendships' effect on health is based on research on humans, elephants are an excellent species to study next. Like humans, they are long-lived, highly social and intelligent animals. We also already know of some similarities in the effects of relationships between humans and elephants. The grandmother effect, or higher rates of reproduction and offspring survival correlating with the presence of the maternal grandmother, has been found in both species (Lahdenperä et al. 2016a). This means having relatives in close proximity has a significant effect on elephants in at least one way. The effects of social isolation has also been studied in Asian elephants previously: Vanitha et al. (Vanitha et al. 2011) found that captive elephants housed in social isolation exhibited more atypical behaviours, or stereotypies.

The aim of this work is to look at how having (social individuals) or not having (solitary individuals) friends, and having or not having relatives as friends, affects several health variables (see Methods for full list) in a semi-captive population of Asian elephants. The most potentially interesting of these health variables are cortisol and the ratio of the white blood cells heterophils and lymphocytes, both of which measure stress along with blood pressure and heart rate, and total white blood cells, which, if high, would indicate infection. Also high total blood protein could indicate infection, but depending on which type of protein is elevated, the reasons behind the elevation can vary widely.

2. Methods

2.1. Data

2.1.1 Study population

This thesis is based on previously collected data. The study population is a semi-captive population of Asian timber elephants for Myanmar, owned by the Myanmar Timber Enterprise (MTE). The elephants work in forest camps as riding, transport and draft animals (Zaw 1997). The data is from elephants located in the regions of Katha

and Kawlin. The adult elephants work five days per week in work groups of typically 6 or 7 individuals. They have a period of rest during the hot season from March to June. Female elephants are relieved from work duties half way through pregnancy until their calf is one year old (Lahdenperä et al. 2016b). During the night the elephants are free to roam in their natural forest habitat undisturbed and their feeding, mating and associating with conspecifics during this time is completely unmanaged by humans. Each elephant has a mahout, or rider or handler, who works with the elephant and retrieves it from the forest in the morning. Mortality and fertility rates in the population generally resemble those reported for wild elephant populations (Clubb et al. 2008). All the younger individuals have been born in semi-captivity, but many of the old elephants have been captured from the wild.

Each elephant has a name, an ID and a log-book, where the basic information about age, sex and origin (wild-caught or captive-born) is recorded, and based on which (matrilineal) pedigrees can be built. These can be used to calculate the relatedness of different individuals. Morphological data about size, body mass and health data are also collected for the elephants during monthly veterinary checks. These records have been kept on the individuals of the population for decades. Thus from this population there exists comprehensive longitudinal data on life-history and health that is unique in the world.

2.1.2 Collection of friendship data

Data on sociality and the relationships between the elephants was collected using questionnaires given to the elephants' the mahout. They were asked if their elephant is solitary (does not interact with other elephants) or social (interacts with other elephants), and if their elephant is social, with which other elephants is their elephant mostly seen associating during work days and in the mornings when they are retrieved from the forest. These individuals were considered friends of the focal elephant. The questionnaires were conducted each year from 2014 to 2018. The answers used are collected at the end of March or beginning of April. In 2018 questionnaires were also conducted in August, but in order to avoid a possible source of uncontrolled variation in the health data caused by the differing season, only data from March-April was included.

2.1.3 Collection of health data

Data on the health variables is from measurements taken within six weeks of the date of the friendship questionnaires. The health variables (except blood pressure, heart rate and mass) were measured from blood or fecal samples.

Observations of 42 different variables relating to health had been measured. Some of these were excluded from the analyses. The concentrations of different electrolytes in the blood were not used, since they are more likely to tell about diet than health. Morphological measures of size, such as height, length and foot circumference, which don't tell about the current health of the elephant, were also excluded. Of the size measures only body mass was used as the per cent difference between the observed mass and the mass expected for age, previously calculated based on data from the same population (Mumby et al. 2015). There were also some variables that measured essentially the same thing, and for each group one was chosen to be used in the analyses. After these exclusions, the remaining 16 variables were included in the analyses. These were alkaline phosphatase, creatinine kinase, creatinine, blood glucose, hematocrit, total protein in blood, triglycerides, total white blood cells, the ratio of heterophiles to lymphocytes, heart rate, diastolic and systolic blood pressures, fecal nematode egg count, presence or absence of trematode eggs in fecal sample, cortisol in feces, and the deviation from expected body mass. While there is no known reason why friends would affect all of these variables, the aim was to get as complete an understanding of whether friends have an effect on health, and so all the variables that could tell about current health were included. The number of observations for each health variable varied between 64 (blood pressure) and 276 (nematode egg count) (mean n of observations 168.5). In total there were 2696 observations of health variables.

Blood samples from the elephants were collected from an ear vein and refrigerated in 4-6°C until they were analysed in a laboratory, a maximum of 24 hours later. White blood cells were counted manually using Turk's solution. A ACCU-Chek® Aviva glucometer was used to obtain the glucose levels. A VetScan i-Stat® 1 was used to get the hematocrit levels. For the rest of the variables measured from the blood, centrifuged serum samples were frozen in -20°C and later analysed in a laboratory using IDEXX VetTest®. Blood pressure was measured from the base of the tail. The elephants were weighed using Eziweigh 3000 scales. For a more accurate description of these collection methods, see dos Santos et al. (in press).

The two parasite variables and cortisol were analysed from fecal samples. Cortisol was

extracted using a validated protocol for boiling extraction and enzyme immunoassay. The inter- and intra-assay coefficients of variation were 12% and less than 10%, respectively, and the minimal detection sensitivity was 0.11 ng/ml. Nematode parasite egg count was obtained by preparing the fecal sample using the McMaster method and manually counting the eggs under a microscope (for more detail see Lynsdale et al. 2015). Trematode presence or absence was determined by using the same McMaster solution. The solution was left to sediment, after which most of the liquid on the top was removed, the sediment was dyed with methylene blue, and the sample was viewed under the microscope to find any possible trematode eggs.

2.1.4 Study outline and sample size

The social questionnaires originally included 384 observations. 14 of these were from August of 2018, and were discarded from analysis to avoid variation in health data caused by differing seasons. Two observations were of babies who were still with their mothers, and for whom no health data had been collected. 38 of the observations were repeated measures of the same individuals from the same year. These were cases where the social questionnaire had been answered multiple times for the same elephant, by one mahout or by different mahouts within a few days. The repeats were taken out, so that only one observation was used per elephant per year. When choosing which data to use, the answers of the mahout closest to the elephant were chosen. If all answers are from the same mahout, the row with highest number of friends was chosen with the assumption that some friend or friends were simply forgotten when filling the questionnaire one time. In most of these cases the answers were identical, in which case one was removed.

The final data used in the analyses had 330 observations from 221 individuals. For 147 individuals there was data from only one year, for 43 from two years, for 27 from three years and for four individuals there was data from four years. There were 212 observations from females and 118 from males. The age range in the data is from 4 to 71 years (mean 25.7 years).

There were 7 elephants for which information only existed that they are social, but the number or identity of the friends had not been provided. The number of friends varied between 0 and 5 (median 1, mean 1.5, see Figure 1). This number does not include babies who were still with their mothers and may be counted as friends of the mother, since they spend all their time together. The data on the number of friends used in the

analyses was categorized into 0, 1, 2, and 3 or more friends, because individuals who had more than three friends were too few to be used as groups of their own. The total number in the 3+ friends group was 61 (47 females, 14 males).

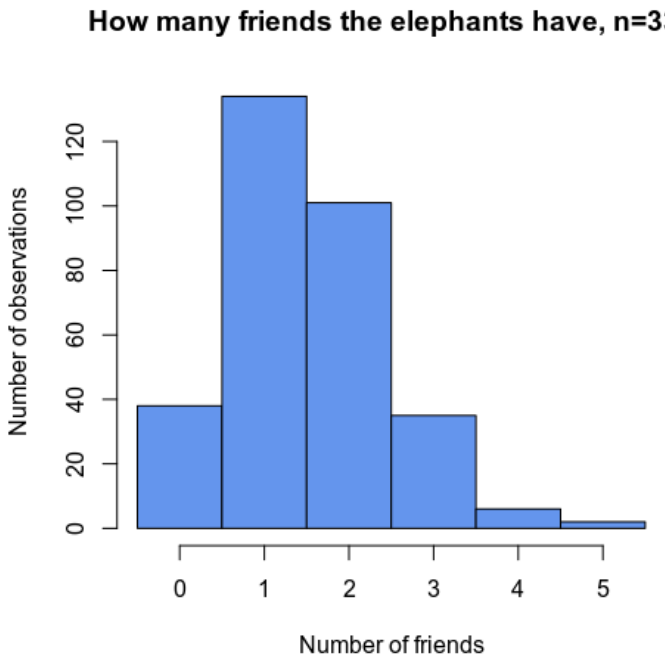

Figure 1. The number of observations with different numbers of friends.

Data on the work group sizes and compositions exist for only 254 observations. This means that when this data is used in the models, the number of observations in reality used in the model is lower.

43 individuals (59 observations) in the data have been caught from the wild. All these individuals are 37 years of age or older (mean 51). The captive-born individuals (271 observations) are almost exclusively younger individuals (mean 20 years, only 44 observations 37 years or older).

In 46 observations the focal elephant had a relative as a friend. 37 of these are mothers with babies. The mother-baby pairs are included in this analysis, since otherwise the number of observations would simply be too small. In 10 of these cases the baby was still under one year old. In the remaining 9 observations of elephants with relatives as friends, there are 4 females and 5 males. In five cases the friend was the focal elephant's mother, but the focal elephant was already old enough (5-11 years of age) to have gone through the taming process, which is when the calves are separated from

the mothers and after which the young elephants being working. Three females were friends with their maternal sisters. One was friends with his mother's male cousin.

2.2. Statistics

All analyses were done on RStudio (R version 3.4.4).

The main objective in this thesis was to investigate the potential effects of having friends on any of the health variables. To do this, I created linear mixed models with each of the health variables as the dependent variable and a two-level variable of whether the focal elephant has friends or not (from here on referred to as "solitary-variable"). The default model included sex, age, work group size as other independent variables and as a random term the work group ID.

It is reasonable to assume that many health variables may have different base levels in different sexes, so that is included as a controlling variable in the model (dos Santos et al. in press). Age is a factor known to affect health in essentially all living beings. Work group size is included to account for the amount of social interactions the elephants have during the work days. The work group size was categorised into three: small (<6 individuals), medium (6-7) and large (>7), based on the default group size of 6-7. The work group ID was included to control for both spatial effects (one work group is located in one place) as well as for the particular working conditions the elephants face. In the case of the two variables on parasites in fecal samples also the most recent deworming date before the measurement was included in the models.

The default model wasn't usable for all health variables, because having so many independent variables often caused problems with either convergence of the model, singular fit or both. In these cases some of the variables were removed to simplify the model. The first variable that was removed was work group size, which seems less likely to affect health than sex, age or environmental factors. If a problem still existed, the random variable of work group ID was removed, because the variable increased the degrees of freedom by 20 - 40, depending on health variable. In these cases work group size was added back to the model, when possible. The only models where neither of the work group variables were included were three of the four models of parasite variables, which included the additional variables of previous deworming dates.

Because in nature the sociality of male and female elephants is known to differ (Vidya & Sukumar 2005), I tested the significance of the interaction between sex and solitary. However, for many of the health variables the sample sizes were simply too small in the solitary group for proper analysis. The limit used was a minimum of 7 elephants in both solitary females and males. If there were fewer individuals, the interaction was left off the model. For health variables with enough data, I performed an ANOVA on the two models, with and without the interaction, to see if the interaction was significant. When the interaction was significant, the interaction was kept in the model for further analyses.

For health variables with a significant difference between the solitary and social individuals, a further analysis was performed with the same model, but using the number of friends as the main independent variable. This was to find any further differences between groups of different numbers of friends, or only between the solitary and social groups.

In order to see if having relatives as friends affects the health of the elephants, a third analysis was run with the same model. In these models the solitary-variable was replaced with another two-level variable relatives/no relatives as friends. Only elephants with friends were included in this analysis. Because the total number of males with relatives as friends in the whole data was 5, the interaction with sex was not included in this analysis.

Because for 74 individuals there is data from multiple years, using focal ID as a second random variable would have been necessary. However, this created too many levels with too few observations in a random variable for any of the models to work. To avoid problems of autocorrelation caused by the same individuals being in the data multiple times, a random subset of data was selected that only included one point of data for each elephant. This was done separately for each variable from an already selected data that only included observations for which there was data for that variable. This was to ensure that in each analysis was included data from each individual that had that variable measured at least once.

Model validation was performed by visual inspection of q-q plots to ensure that the residuals of all LMMs adhered to the distribution used in each model. Most of the health variables did not significantly deviate from gaussian distribution. For cortisol, triglycerides and the heterophil-lymphocyte ratio the distribution deviated statistically

significantly from the gaussian distribution. However, based on the visual examination of the q-q plots these deviations were not large, and for each of these all alternative distributions had a clearly worse fit, so they were also analysed assuming gaussian distribution. Alkaline phosphatase and fecal nematode egg count followed a negative binomial distribution, and the presence/absence of trematodes in feces was binomial. For these, three a generalised linear mixed models were used with the correct distributions. A summary of variables and distributions used in the analyses for each variable can be found in appendix 1.

For those health variables where results suggested a difference between some of the groups of interest, I calculated least square means (ls means) for the groups. These were compared using the Tukey method to see if there were significant differences between the different groups.

3. Results

3.1 Total protein

The total protein level was on average 7.59 g/dl (range 5.7-9.8 g/dl, n=67) for males and 7.89 (range 5.7-9.9, n=113) for females. This was the only health variable where the effect of friends depended on the sex of the elephant (interaction between sex and solitary-variable, was significant in the model, p=0.029). The solitary males had significantly higher total protein levels than social males (difference in ls means 0.5043, SE 0.174, p=0.025, figure 2a, table 1). The levels did not differ statistically between social and solitary females (difference in ls means 0.0284, SE 0.205, p=0.999, figure 2a, table 1). When the model was run with the number of friends, it also showed a significant difference between solitary males and each of the groups of different numbers of friends (table 5b in appendix 2). However, when the pairwise comparisons were made with ls means and the p-values adjusted to take into account the multiple comparisons, the differences became insignificant (table 1, figure 2b). The total protein was not affected by the presence of relatives as friends (table 5c in appendix 2, figure 2c).

Table 1. The results of pairwise comparisons of different groups for total protein. The first part is the comparisons of solitary(sol) / social(fri) for different sexes (f/m). The second part is comparisons of different number of friends for different sexes.

comparison	**estimate**	**SE**	**df**	**t-ratio**	**p-value**
fri,f – sol,f	0.0284	0.205	75.7	0.138	0.999
fri,f – fri,m	0.2367	0.114	58.7	2.07	0.175
sol,f – sol,m	-0.296	0.218	77.5	-1.359	0.529
fri,m – sol,m	-0.5043	0.174	65.3	-2.906	0.025
comparison	**estimate**	**SE**	**df**	**t-ratio**	**p-value**
0,f - 1,f	-0.0435	0.223	68.1	-0.195	1
0,f - 2,f	0.0413	0.225	72	0.184	1
0,f - 3+,f	0.0249	0.259	68.7	0.096	1
1,f - 2,f	0.0848	0.155	76.5	0.547	0.999
1,f - 3+,f	0.0684	0.201	73.5	0.34	1
2,f - 3+,f	-0.0164	0.193	77	-0.085	1
0,f - 0,m	-0.2827	0.225	73.4	-1.255	0.912
1,f - 1,m	0.1841	0.182	66.8	1.01	0.971
2,f - 2,m	0.228	0.209	49.8	1.089	0.956
3+,f - 3+,m	0.3627	0.242	59.2	1.501	0.804
0,m - 1,m	0.4233	0.202	60.2	2.1	0.427
0,m - 2,m	0.5521	0.236	76.9	2.344	0.284
0,m - 3+,m	0.6703	0.236	76.4	2.844	0.099
1,m - 2,m	0.1288	0.226	67.7	0.57	0.999
1,m - 3+,m	0.247	0.229	74.7	1.079	0.959
2,m – 3+,m	0.1183	0.251	48.3	0.47	0.999

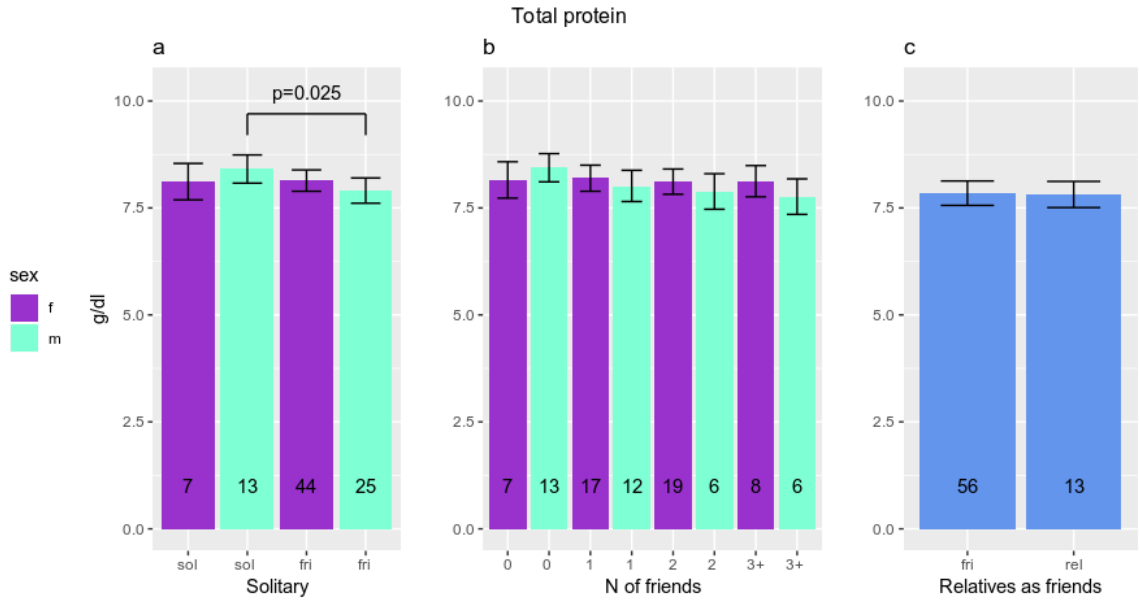

Figure 2. The least square means of different groups for total protein. The error bars show 95% confidence intervals. The number at the bottom of each bar is the number of observations in that group. All significant differences shown by pairwise comparisons are marked in the figure. a) For solitary (sol) / social (fri), for each sex. b) For different numbers of friends, for each sex. c) For whether the elephant has relatives in their friends (rel) or no (fri).

3.2 Cortisol

The cortisol level was on average 86.94 ng/g of feces (range=24.18-264.91 ng/g, n=136). For cortisol there was a significant difference between the solitary and social groups (table 6a in appendix 2). The difference in ls mean between solitary and social groups was 56.4 ng/g (SE=12.2, p<0.001), with solitary individuals having higher cortisol. A significant difference in the same direction was found using the number of friends, so that the solitary group had higher cortisol levels than any of the groups with friends. There was no differences between the groups that did have friends (table 2, table 6b in appendix 2) Additionally, the individuals who had relatives as friends had a cortisol level 20.9 ng/g (SE=8.26, p=0.014) higher than those who did not (figure 3c).

Table 2. The pairwise comparisons of groups of different numbers of friends for cortisol.

comparison	estimate	SE	df	t-ratio	p-value
0 - 1	48.36	12.82	69	3.773	0.002
0 - 2	50.87	12.99	68	3.916	0.001
0 - 3+	39.41	14.13	69.4	2.789	0.034
1 - 2	2.51	7.74	62.4	0.324	0.988
1 - 3+	-8.95	9.59	67.9	-0.934	0.787
2 - 3+	-11.46	8.32	61	-1.378	0.518

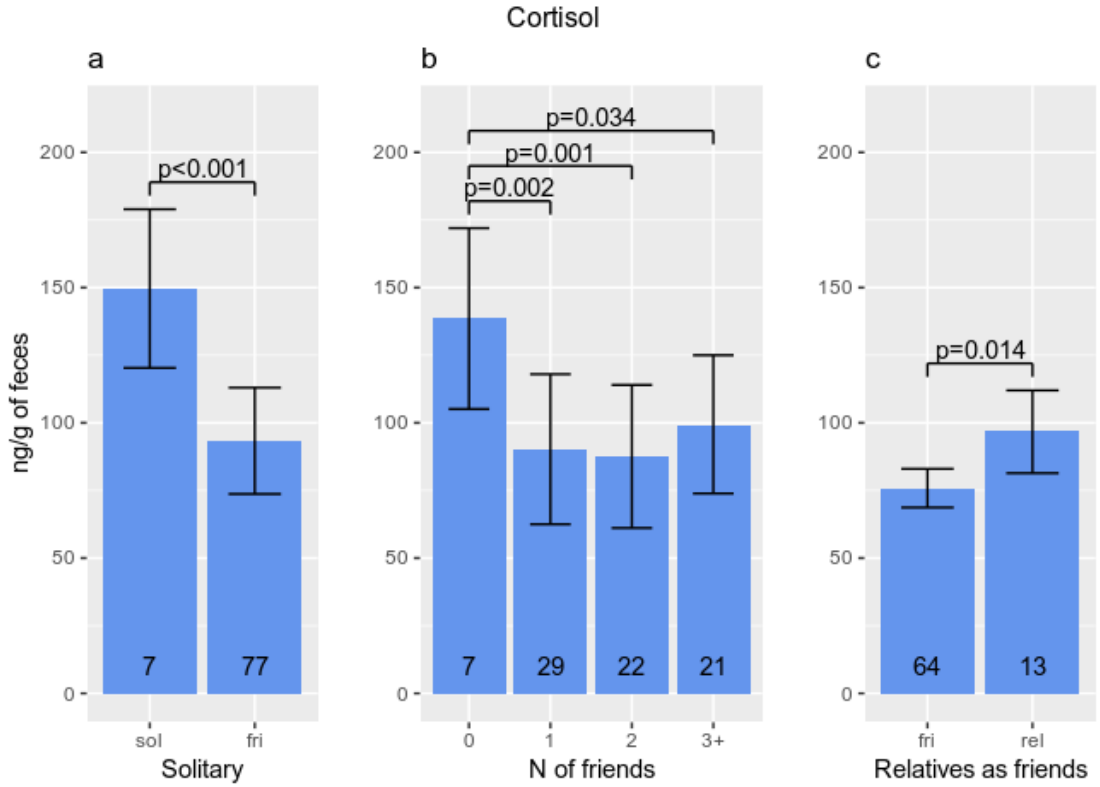

Figure 3. The least square means of different groups for cortisol. The error bars show 95% confidence intervals. The number at the bottom of each bar is the number of observations in that group. All significant differences shown by pairwise comparisons are marked in the figure. a) For solitary (sol) / social (fri). b) For different numbers of friends. c) For whether the elephant has relatives in their friends (rel) or no (fri).

3.3 Mass relative to expected

The body masses in the data had a mean of 2082 kg (range 893-3850 kg). When the

expected masses based on age were calculated for the elephants, the deviation in from the expected ranged between 38% lighter and 67% heavier than expected. Friends did not have a significant effect on the relative mass (figure 4a, table 7a in appendix 2). However, relatives as friends had a significant effect on relative mass, so that elephants with relatives were heavier (difference in ls means 0.0763, meaning the individuals with relatives as friends were on average 7.6% heavier, SE 0.0323, p=0.020, figure 4b, table 7b in appendix 2).

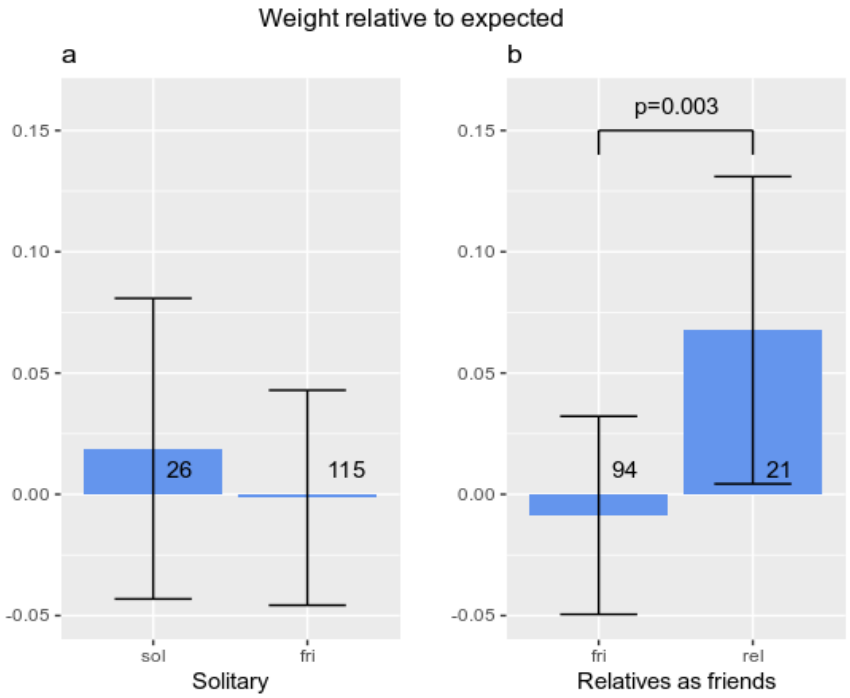

Figure 4. The least square means of different groups for mass relative to expected. A value of 0.05, for example, means that the elephant is 5% heavier than expected for its age. The error bars show 95% confidence intervals. The number on the bar shows the number of observations of that group. All significant differences shown by pairwise comparisons are marked in the figure. a) For solitary (sol) / social (fri). b) For whether the elephant has relatives in their friends (rel) or no (fri).

3.4 Presence or absence of trematode parasites

Trematode parasites were found in the feces of 50.7% of the elephants (n=195). Friends did not have a significant effect on the presence of parasites (figure 5a, table 8a in appendix 2). However, relatives as friends had a significant effect on the parasites, so that elephants with relatives were less likely to have parasites (difference in ls means 0.332, p=0.020, figure 5b, table 8b in appendix 2).

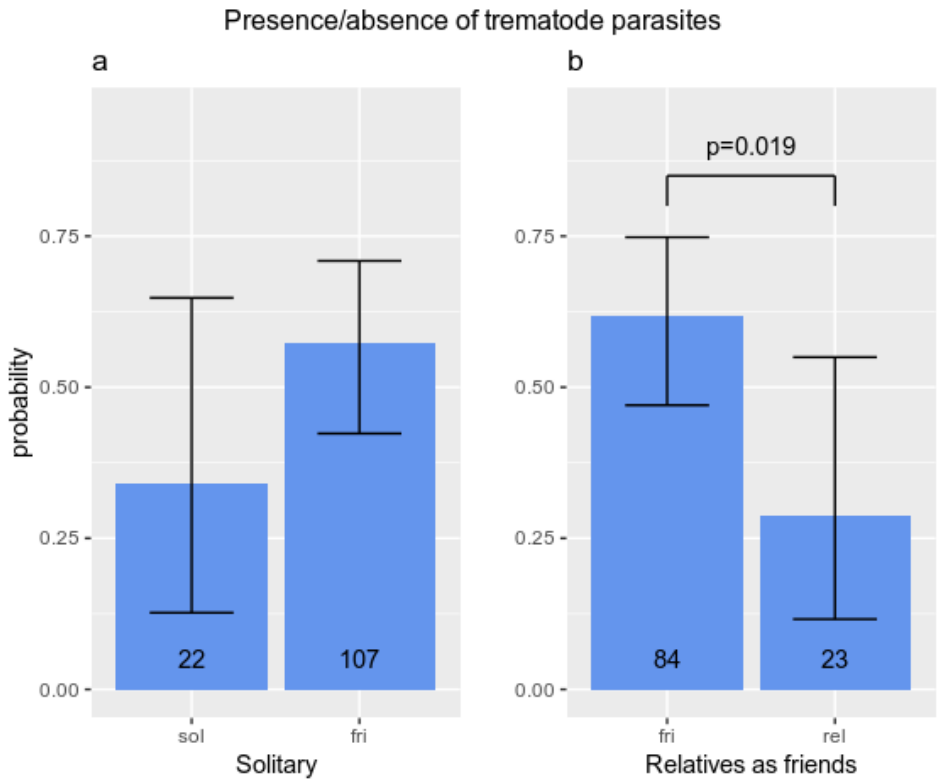

Figure 5. The least square means of different groups for presence/absence of trematode parasites in feces. The error bars show 95% confidence intervals. The number at the bottom of each bar is the number of observations in that group. All significant differences shown by pairwise comparisons are marked in the figure. a) For solitary (sol) / social (fri). b) For whether the elephant has relatives in their friends (rel) or no (fri).

3.5 Systolic blood pressure

The systolic blood pressure was on average 131.4 mmHg (range 72-190 mmHg, n=64). Friends did not have a significant effect on systolic blood pressure (figure 6a, table 9a in appendix 2), but relatives as friends did, so that elephants with relatives had on average a lower systolic blood pressure (difference in ls means 26.7 mmHg, SE 8.22, p=0.003, figure 6b, table 9b in appendix 2). A nonsignificant difference in the same direction is also seen in diastolic blood pressure (table 10 in appendix 2)

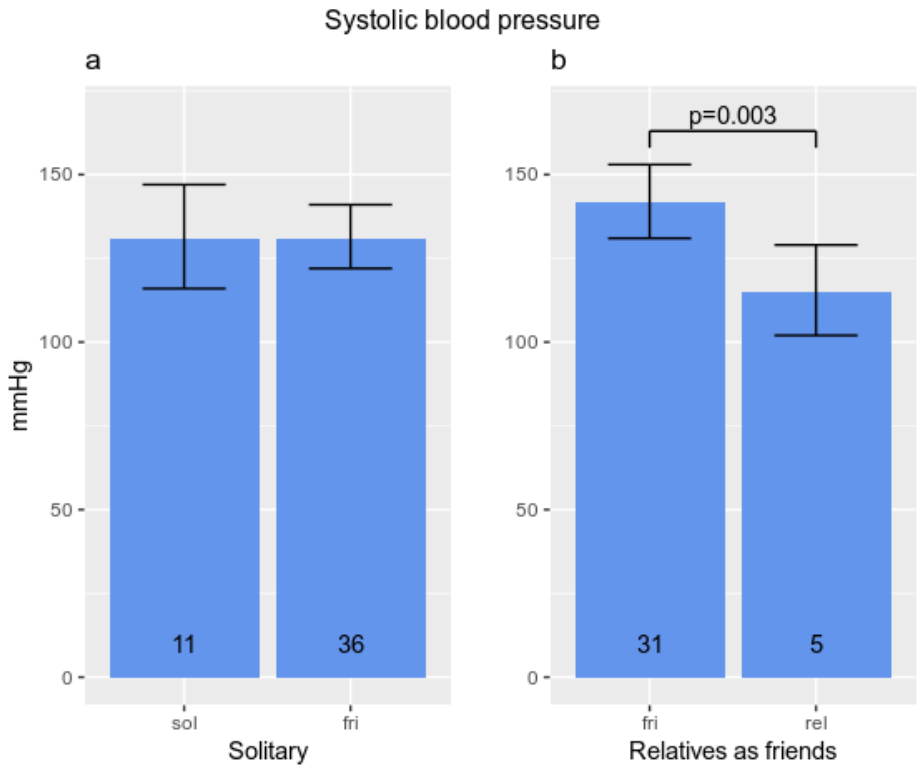

Figure 6. The least square means of different groups for systolic blood pressure. The error bars show 95% confidence intervals. The number at the bottom of each bar is the number of observations in that group. All significant differences shown by pairwise comparisons are marked in the figure. a) For solitary (sol) / social (fri). b) For whether the elephant has relatives in their friends (rel) or no (fri).

3.6 Other health variables

Neither solitary nor relatives significantly explained any variation in the other 11 health variables. The averages and ranges for these variables can be found in table 3. For full results of the models for all health variables, see appendix 2, tables 5-20.

Table 3. The averages and ranges of the 11 health variables with no significant differences

Variable	Unit	Average	Minimum	Maximum	N
Alkaline phosphatase	U/L	100.2	37	322	180
Heart rate	Beats per minute	35.46	24	77	96
Creatine kinase	U/L	173.9	28	700	180
Creatinine	mg/dl	1.022	0.4	2.1	180
Diastolic bp	mmHg	95.47	53	127	64
Nematode parasites	N of eggs / g	10.92	0	272	276
Glucose	mmol/l	4.044	2.0	5.9	180
Hematocrit	%	35.09	24	50	180
Triglycerides	mg/dl	11.25	0	53	180
Total white blood cells	million/l	15386	6622	27500	180
Ratio of heterophils and lymphocytes		1.01	0.32	5.33	158

3.7 Other independent variables in the model

Age was the independent variable most commonly significant in the models, explaining variation in six variables (total protein, number of nematode parasite eggs in feces and, in the model with relatives, hematocrit increasing with age, alkaline phosphatase, heart rate and total white blood cells decreasing with age).

Work group size had a significant effect on mass relative to expected (those in medium-sized groups were lighter than those in big groups), total protein (those in medium-sized groups had lower total protein than those in big groups) and systolic blood pressure (those in medium-sized groups had lower blood pressure than those in big groups in the relatives-model).

Time since last deworming had a significant effect on nematode but not trematode parasites. Unsurprisingly, the number of parasite eggs increased when more time had passed since the previous deworming.

For full results of the models for all health variables, see appendix 2, tables 5-20.

4. Discussion

Sociality has been widely studied in a huge variety of animals, in multiple points of view. Social structures and their effect on for example stress (for example Creel 2001; Kikusui et al. 2006) and reproduction (for example Cameron et al. 2009; McGuire et al. 2002) have been studied in multiple species. These studies have found social relationships to be beneficial for individuals. However, friendships' effect on health has mostly only been studied in humans. The aim of this study was to find out if friends have an effect on the health of Asian elephants in a semi-captive population.

In the analyses I found a significant difference in the total protein levels in blood in solitary and social males, so that social males had lower total protein. This difference was not present in females. Cortisol levels were higher in solitary elephants than elephants who had any number of friends. Also individuals who had relatives as friends had higher cortisol than those who didn't. I also found that the elephants with relatives as friends were heavier, had less trematode parasites and lower systolic blood pressure. Throughout the interpretation of these results has to be kept in mind, that during the analyses, 34 different models were run. With this amount of tests, it is not unlikely that some of the p-values are significant due to coincidence, and there is no true difference between some of the groups studied where a difference was found. Another important point is that from this data, only correlations between the variables can be found: causation, and the direction of possible causation, cannot be reliably inferred.

For total protein in blood, the ls means of both females and males are well within their reference intervals, the range of values deemed normal (6.8-8.9 g/dl in females, 6.6-8.7 g/dl in males) (dos Santos et al. in press). So, while the mean total protein for the solitary males isn't unexpectedly high, it is significantly higher than that of the social group. The reason for this is not clear. This is partly due to the fact that depending on which kinds of proteins are elevated, the interpretation can be very different. For example, if the increase is due to globulin proteins, or antibodies, it probably tells about an ongoing infection or wound. In this case, being solitary would have a direct link to the health of the elephant. However, an increase in different kinds of proteins, such as albumins, would indicate completely different reasons. The reason can also be

environmental. When an individual is dehydrated, there will be less water and more protein in the same volume of blood, increasing total protein.

The higher cortisol levels in solitary as opposed to social elephants is exactly the kind of result that would be expected: for a social animal, being socially isolated increases stress (for example Detillion et al. 2004; Hatch et al. 1965; Silk 2014). This is the only instance in the results here where a previously established causational relationship is known between the variables studied (Hatch et al. 1965), and thus it is possible to be fairly certain that being socially isolated is the cause for the higher cortisol levels. While stress itself doesn't necessarily tell about the health of the individual, being stressed for long periods of time can have significant, negative effects on health by constantly keeping the body in a state of disequilibrium, which increases the risks of many diseases (McEwen 2008)

All the other differences identified here were between elephants with relatives as friends and elephants without relatives as friends. This variable was used in attempt to quantify the quality of the relationship. In the wild, Asian elephants usually spend time in groups that consist of relatives (Vidya & Sukumar 2005). It has also been found before that having the mother's relatives in close proximity as the calf is young increases calf survival (Lahdenperä et al. 2016a). This, as well as kin selection, makes it reasonable to think that maybe, if having friends does affect the health of elephants, having relatives as friends would affect the health more than having non-related elephants as friends. However, in these analyses it is notable, that in 80% of the cases in the data, the related friend is in fact the focal elephant's own baby. In order to get a more reliable result on whether having relatives as friends does have an effect, it would have been better to exclude the mothers from the analyses. However, this would have resulted in not having enough observations to do the analysis at all, and thus the mothers were also included.

What is interesting is that the same group in which cortisol level is higher, systolic blood pressure is lower, despite the fact that at least in humans stress has been found to contribute to high blood pressure (Kulkarni et al. 1998). The ls means for systolic pressure in each group are within reference intervals previously calculated from data on the same population that was studied here, so none of the groups as a whole has high or low blood pressure. There were individuals in the data, however, that had systolic blood pressure higher or lower than that included in the reference interval (range of values in this data 80-154 mmHg for elephants with relatives as friends, n=5,

and 72-190 mmHg for elephants without relatives, n=31, the reference interval 99-166 mmHg) (dos Santos et al. in press). This would suggest that even though the difference in blood pressure between the groups is statistically significant, the practical difference isn't necessarily big enough to be relevant for the health of the elephants.

We see a similar pattern in parasite load as in blood pressure: the parasite load is lower in the group that has relatives as friends and higher cortisol levels. And, akin to high blood pressure, higher parasite loads are often linked with higher cortisol levels. A link between cortisol and parasites has been found in for example cliff swallows (*Petrochelidon pyrrhonota*), treefrog tadpoles (*Hyla versicolor*), black iguanas (*Ctenosaura similis*) and chimpanzees (*Pan troglodytes schweinfurthii*) (Belden & Kiesecker 2005; Hanley & Stamps 2002; Muehlenbein & Watts, 2010; Raouf et al. 2006). The fact that both blood pressure and probability of having parasites are in these results negatively correlated with fecal cortisol levels is an interesting finding.

Friends didn't seem to have an effect on some of the potentially most interesting health variables. There was no difference between groups in heterophil/lymphocyte ratio or heart rate. There were also no differences in total white blood cells, although it is plausible that no difference was seen there, because both low and high white blood cells tell about health problems. If friends create health benefits, the difference in white blood cell count might be in variation of the groups instead of the means.

The differences found here between solitary and social individuals suggest that friends do have at least some effect on health in Asian elephants. There could potentially be an even stronger and more encompassing link between health and friendships than seen here. There are multiple reasons why this data might not have shown the health benefits of friends, even if they exist.

First of all, the friendship data is based on the mahouts' memory. The human memory is quite fallible, and the mind is excellent at finding patterns even if there were none (Eysenck 2012). This means that the way this data was collected inevitably results in data that is less reliable than data collected as the elephants are observed together would be. However, since the mahouts know their elephants very well, this is probably the most reliable data that it is possible to get from a population of Asian elephants. Unlike the elephants on savannas in Africa, Asian elephants living in a forest (Fernando & Lande 2000) are very difficult to observe, and it can't be expected that the mahouts would write down every morning which of the elephants are together when they are

fetched for the work day, even though that would give us a more objective measure of how much the different elephants really do spend time together.

Secondly, the only species in which the relationship between friends and health seems to have been studied in before this is humans. Those human studies are done in a slightly different way than this one. Instead of looking at single variables of health, they have mostly focused on disease risks (such as coronary heart disease and stroke, Valtorta et al. 2016, and dementia, Holwerda et al. 2014) and mortality (Holt-Lunstad et al. 2010). This is a different kind of approach to health, one that isn't looked at here. Of Sartorius' (2006) definitions, this study was mostly focusing on the third one: equilibrium within an individual, while disease and the ability to cope with daily life were not studied at all. It is possible, that even if based on this data there doesn't seem to be many differences in health between the groups of different numbers of friends, there would be a difference in for example disease risk or mortality, if a longer-term study was conducted and data different to this was used for the elephants. Also, because of this difference in approach to health between this and many other studies, comparing the results of these studies is tricky.

Thirdly, at least in humans being alone and being lonely are two very different things, and have found to not be correlated (Coyle & Dugan 2012). A person can feel lonely even with an active social life, while someone else might be perfectly content with spending most of their time alone. For example for the risk of dementia loneliness, instead of social isolation, is the key factor (Holwerda et al. 2014). Of course, just because this is the case in humans, does not mean that it is also the case in elephants. However, it could be, and it is impossible to find out, since there is no way ask the elephants if they are feeling lonely. If it is the case also in elephants that social isolation and feeling lonely do not correlate, then it is possible that data such as this that only includes the number of elephants an individual spends time with will not find any differences, even if they are there.

Despite these shortcomings, this thesis and the population studied here offer at present unique insight to how the sociality or loneliness in non-human animals may affect health. Obtaining data such as this is often impossible for large mammals outside zoo settings, which is a substantially different environment than that in which wild or even semi-captive populations such as this live. While through field observations it is in some cases (such as in that of the elephant population in Amboseli national park, Moss et al. 2011) possible to get extensive objective data on the social structures and relationships

in a wild population, combining that with equally extensive longitudinal health data is only possible in a population such as this one, and, to my knowledge, has not been done before outside a laboratory or a zoo. While the differences in health between social and solitary individuals found here were not many, they existed in meaningful variables, which suggests there may be a significant link between health and sociality in elephants.

Studies aiming to understand the effects friends have on the health of Asian elephants can help with management of the animals in full captivity in zoos around the world, since they can help determine what kind of groups they should be kept in in order to keep the animals as healthy as possible in captivity. Also in a semi-captive population such as this one, understanding the effects of sociality can help keep the animals healths, as well as aid with population management. Having a better understanding of the effects of sociality and social isolation can also help guide conservation efforts of this endangered (Choudhury et al. 2008) species. While results based on elephants can not necessarily be extended to other species, this study and others like it will give a broader understanding of sociality and its effects on large, social animals.

Further research is required to better understand the full extent to which sociality or loneliness has an effect on health of elephants. This future research could, for example, study mortality in relation to the number of friends, as well as looking at disease risks or reproduction. It would also be interesting to compare elephants who have long-term relationships to those who change friends more often, to see if there is an effect of stable, long friendships on health. This would require having data from a longer time period that the one used here, as well as a lot more repeats for all of the elephants during the study period.

Acknowledgements

I had three supervisors, Virpi Lummaa, Mirkka Lahdenperä and Martin Seltmann, without whom this thesis would have been impossible.

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Appendices

Appendix 1

Table 4. The models and distributions used for each health variable. Solitary refers to two-level variable of whether the elephant has friends or is solitary. Relatives refers to the two-level variable of whether the elephant has relatives as friends or not. Friends refers to the four-level variable of how many friends the elephant has. Wg_groupsize and wg_groupID refer to the work group size and ID. Sed_worm_date and fec_worm_date are time since last deworming at the time of fecal sample collection from which the parasite data is.

health variable	**primary fixed variable**	**other fixed variables**	**random variable**	**distribution used**
mass relative to expected	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
mass relative to expected	relatives	sex, age, wg_groupsize	wg_groupID	gaussian
cortisol	friends	sex, age, wg_groupsize	wg_groupID	gaussian
cortisol	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
cortisol	relatives	sex, age	wg_groupID	gaussian
heart rate	solitary	sex, age, wg_groupsize		poisson
heart rate	relatives	sex, age, wg_groupsize		poisson
alkaline phosphate	solitary	sex, age, wg_groupsize		negative binomial
alkaline phosphate	relatives	sex, age, wg_groupsize		negative binomial
creatine kinase	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
creatine kinase	relatives	sex, age,	wg_groupID	gaussian

		wg_groupsize		
creatinine	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
creatinine	relatives	sex, age, wg_groupsize	wg_groupID	gaussian
diastolic bp	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
diastolic bp	relatives	sex, age, wg_groupsize	wg_groupID	gaussian
glucose	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
glucose	relatives	sex, age, wg_groupsize	wg_groupID	gaussian
hematocrit	solitary	sex, age, wg_groupsize		gaussian
hematocrit	relatives	sex, age, wg_groupsize		gaussian
total white blood cells	solitary	sex, age, wg_groupsize		gaussian
total white blood cells	relatives	sex, age, wg_groupsize		gaussian
systolic bp	solitary	sex, age, wg_groupsize		gaussian
systolic bp	relatives	sex, age, wg_groupsize		gaussian
total protein	friends	sex, age, wg_groupsize	wg_groupID	gaussian
total protein	solitary	*sex, age, wg_groupsize	wg_groupID	gaussian
total protein	relatives	sex, age, wg_groupsize	wg_groupID	gaussian
triglycerides	solitary	sex, age, wg_groupsize	wg_groupID	gaussian
triglycerides	relatives	sex, age,	wg_groupID	gaussian

		wg_groupsize		
heterophil/ lymphocyte ratio	solitary	sex, age	wg_groupID	gaussian
heterophil/ lymphocyte ratio	relatives	sex, age	wg_groupID	gaussian
nematode egg count	solitary	sex, age, fec_worm_date		negative binomial
nematode egg count	relatives	sex, age, fec_worm_date		negative binomial
trematode p/a	solitary	sex, age, sed_worm_date	wg_groupID	binomial
trematode p/a	relatives	sex, age, sed_worm_date		binomial

Appendix 2

Results of the linear models, by health variable.

Table 5. The linear model results for total protein. a) The linear model run with solitary. b) The model ran with the number of friends. Here the intercept has been changed to be males instead of females. c) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	8.210074	0.261275	37.71106	31.423	< 2e-16
solitary1	-0.02838	0.205247	75.72401	-0.138	0.89039
sexm	-0.23666	0.114305	58.69011	-2.07	0.04282
age	0.010212	0.003785	44.20486	2.698	0.00984
wg_groupsizemedium	-0.59901	0.24177	30.07814	-2.478	0.01907
wg_groupsizesmall	-0.28092	0.302613	47.68711	-0.928	0.35793
solitary1:sexm	0.532657	0.235342	78.46700	2.263	0.02638
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	8.516646	0.27097	27.90943	31.43	< 2e-16
friends1	-0.42331	0.201623	60.16390	-2.1	0.03998
friends2	-0.55208	0.235553	76.92633	-2.344	0.02167
friends3+	-0.67033	0.235683	76.4324	-2.844	0.00571
sexf	-0.28275	0.225226	73.40827	-1.255	0.21332
age	0.009899	0.003811	36.28565	2.597	0.01349
wg_groupsizemedium	-0.61281	0.23836	24.08671	-2.571	0.01674
wg_groupsizesmall	-0.28259	0.30339	33.49281	-0.931	0.35829
friends1:sexf	0.466826	0.271726	74.75300	1.718	0.08994
friends2:sexf	0.510792	0.300495	67.15091	1.7	0.09379
friends3+:sexf	0.645429	0.324822	69.72457	1.987	0.05085
c	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	7.826987	0.361578	37.53645	21.647	<2e-16
relativesrel	-0.02778	0.139268	62.9519	-0.199	0.8426
sexm	-0.26299	0.116152	52.5154	-2.264	0.0277
age	0.008893	0.004004	28.4932	2.221	0.0345
wg_groupsizemedium	-0.15678	0.337983	37.60961	-0.464	0.6454
wg_groupsizesmall	0.106381	0.389397	25.88365	0.273	0.7869

Table 6. The linear model results for cortisol. a) The linear model run with solitary. b) The model ran with the number of friends. c) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	104.5372	17.7461	21.1121	5.891	7.42E-06
solitarysol	56.3626	12.152	77.6893	4.638	1.40E-05
sexm	-0.1937	6.7498	65.4362	-0.029	0.977
age	-0.347	0.2632	50.0529	-1.318	0.193
wg_groupsizemedium	-21.0376	16.844	18.9998	-1.249	0.227
wg_groupsizesmall	10.353	27.3847	17.2767	0.378	0.71
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	139.902	27.4066	41.8781	5.105	7.62E-06
friends1	-48.3632	12.8179	68.9607	-3.773	0.000337
friends2	-50.873	12.9915	67.9555	-3.916	0.000211
friends3+	-39.4085	14.1278	69.3563	-2.789	0.006811
sexm	2.5997	6.6245	52.976	0.392	0.696313
age	-0.123	0.3072	54.561	-0.401	0.690344
wg_groupsizemedium	-13.9716	21.7649	23.8553	-0.642	0.527038
wg_groupsizesmall	14.3304	34.9304	20.373	0.41	0.6859
c	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	81.7547	6.4769	40.373	12.622	1.34E-15
relativesrel	20.9292	8.257	50.3364	2.535	0.0144
sexm	-2.5064	6.293	67.1402	-0.398	0.6917
age	-0.2268	0.2083	36.0468	-1.089	0.2836

Table 7. The linear model results for percentual difference between observed and expected mass. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	8.05E-02	4.17E-02	3.60E+01	1.931	0.0614
solitary1	2.02E-02	3.13E-02	1.25E+02	0.646	0.5197
sexm	-7.72E-04	2.33E-02	1.15E+02	-0.033	0.9737
age	-8.90E-04	7.99E-04	8.47E+01	-1.114	0.2685
wg_groupsizemedium	-8.22E-02	3.48E-02	1.98E+01	-2.363	0.0285
wg_groupsizesmall	-9.29E-02	5.74E-02	4.47E+01	-1.619	0.1124
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	9.87E-03	4.06E-02	3.76E+01	0.243	0.8091
relativesrel	7.63E-02	3.23E-02	1.08E+02	2.365	0.0198
sexm	2.63E-02	2.51E-02	1.02E+02	1.046	0.298
age	-1.66E-04	7.81E-04	5.83E+01	-0.213	0.8321
wg_groupsizemedium	-5.26E-02	3.14E-02	2.02E+01	-1.675	0.1094
wg_groupsizesmall	-3.03E-02	5.49E-02	2.47E+01	-0.552	0.5857

Table 8. The linear model results for presence of trematode parasites. The model used logit as a link function, and the results in this table have not been transformed back. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.17099	0.54941	0.311	0.756
solitary1	-0.95157	0.72801	-1.307	0.191
sexm	0.1889	0.50507	0.374	0.708
age	0.0119	0.01408	0.845	0.398
sed_worm_date	-0.6029	0.57303	-1.052	0.293
b	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	0.356596	0.572402	0.623	0.5333
relativesrel	-1.39851	0.596877	-2.343	0.0191
sexm	0.249934	0.530799	0.471	0.6377
age	0.007553	0.014447	0.523	0.6011
sed_worm_date	-0.38628	0.649263	-0.595	0.5519

Table 9. The linear model results for systolic blood pressure. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	133.9023	11.06499	12.101	4.09E-15
solitary1	-0.03582	8.21738	-0.004	0.997
sexm	-6.34224	5.38632	-1.177	0.246
age	0.02537	0.22514	0.113	0.911
wg_groupsizemedium	-2.27637	9.6908	-0.235	0.815
wg_groupsizesmall	2.40993	12.56599	0.192	0.849
b	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	163.1104	14.3822	11.341	2.26E-12
relativesrel	-26.669	8.2216	-3.244	0.00289
sexm	-13.5715	4.8349	-2.807	0.0087
age	0.1439	0.2461	0.585	0.56307
wg_groupsizemedium	-27.7281	13.0704	-2.121	0.04226
wg_groupsizesmall	-21.2937	15.3916	-1.383	0.17673

Table 10. The linear model results for diastolic blood pressure. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	87.4293	10.933	26.6734	7.997	1.48E-08
solitary1	3.1637	6.8705	40.6785	0.46	0.648
sexm	0.282	3.8693	29.2824	0.073	0.942
age	0.1571	0.2019	36.954	0.778	0.441
wg_groupsizemedium	2.2097	10.0648	22.0687	0.22	0.828
wg_groupsizesmall	8.3125	11.0843	40.0915	0.75	0.458
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	99.71385	17.63942	14.89737	5.653	4.71E-05
relativesrel	-10.8613	8.35759	29.90539	-1.3	0.204
sexm	-5.30191	4.3172	21.40295	-1.228	0.233
age	-0.06569	0.27764	19.35473	-0.237	0.815
wg_groupsizemedium	-2.6193	16.02503	13.98923	-0.163	0.873
wg_groupsizesmall	1.18781	20.4598	11.00393	0.058	0.955

Table 11. The linear model results for alkaline phosphate. The model used negative binomial distribution and log link function. The results have not been transformed back. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	4.798175	0.191817	25.014	< 2e-16
solitary1	-0.07095	0.112631	-0.63	0.5287
sexm	0.157555	0.088367	1.783	0.0746
age	-0.01579	0.002866	-5.508	3.63E-08
wg_groupsizemedium	0.030136	0.173638	0.174	0.8622
wg_groupsizesmall	0.295084	0.213613	1.381	0.1672
b	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	4.74172	0.31664	14.975	< 2e-16
relativesrel	-0.2237	0.14319	-1.562	0.118
sexm	0.13499	0.1018	1.326	0.185
age	-0.01502	0.00344	-4.366	1.26E-05
wg_groupsizemedium	0.11559	0.29645	0.39	0.697
wg_groupsizesmall	0.3562	0.33266	1.071	0.284

Table 12. The linear model results for heart rate. The model uses poisson distribution and log as link function. The results have not been transformed back. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	3.694919	0.094937	38.92	<2e-16
solitary1	-0.056624	0.06236	-0.908	0.3639
sexm	0.004006	0.046111	0.087	0.9308
age	-0.004013	0.001789	-2.243	0.0249
wg_groupsizemedium	-0.071423	0.083445	-0.856	0.392
wg_groupsizesmall	0.017408	0.09847	0.177	0.8597
b	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	3.735463	0.151881	24.595	<2e-16
relativesrel	-0.006147	0.083696	-0.073	0.941
sexm	0.016151	0.052203	0.309	0.757
age	-0.004199	0.0025	-1.68	0.093
wg_groupsizemedium	-0.11597	0.14131	-0.821	0.412
wg_groupsizesmall	-0.026105	0.155023	-0.168	0.866

Table 13. The linear model results for creatine kinase. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	123.3143	46.514	45.8059	2.651	0.011
solitary1	-22.8401	27.2098	68.1128	-0.839	0.404
sexm	-0.7114	19.5425	67.5183	-0.036	0.971
age	0.4909	0.6796	55.0188	0.722	0.473
wg_groupsizemedium	32.0653	42.8627	36.2206	0.748	0.459
wg_groupsizesmall	11.4801	52.1049	53.4998	0.22	0.826
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	73.908	75.6575	32.3895	0.977	0.336
relativesrel	3.6785	32.1374	64.9217	0.114	0.909
sexm	-13.7517	23.9064	55.4529	-0.575	0.567
age	0.6352	0.8149	33.616	0.78	0.441
wg_groupsizemedium	82.1545	70.9583	31.9767	1.158	0.256
wg_groupsizesmall	75.6621	81.7267	25.4846	0.926	0.363

Table 14. The linear model results for creatinine. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	0.892405	0.157861	45.87799	5.653	9.63E-07
solitary1	0.002755	0.093456	58.94552	0.029	0.977
sexm	-0.01206	0.061725	71.37082	-0.195	0.846
age	0.000673	0.002374	50.54086	0.283	0.778
wg_groupsizemedium	0.107791	0.146903	36.99637	0.734	0.468
wg_groupsizesmall	0.081374	0.178951	62.08350	0.455	0.651
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	0.770669	0.259212	29.31031	2.973	0.00584
relativesrel	-0.09996	0.0940467	64.88091	-1.063	0.29179
sexm	-0.06837	0.0756083	56.14555	-0.904	0.36975
age	-0.00073	0.0029823	21.45148	-0.246	0.80781
wg_groupsizemedium	0.304767	0.2414559	27.40681	1.262	0.21751
wg_groupsizesmall	0.323483	0.285325	21.18774	1.134	0.26957

Table 15. The linear model results for nematode parasite eggs in feces. The model used negative binomial distribution and log link function. The results have not been transformed back. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	1.36377	0.305296	4.467	7.93E-06
solitary1	-0.32147	0.407474	-0.789	0.430146
sexm	0.242685	0.30352	0.8	0.423961
age	0.022778	0.008331	2.734	0.006255
fec_worm_date	1.031765	0.300622	3.432	0.000599
b	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	1.243946	0.336072	3.701	0.000214
relativesrel	-0.54661	0.398106	-1.373	0.169745
sexm	0.299379	0.325726	0.919	0.358037
age	0.02042	0.008876	2.301	0.02142
fec_worm_date	1.604509	0.457161	3.51	0.000449

Table 16. The linear model results for glucose. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	4.304159	0.441301	48.90150	9.753	4.68E-13
solitary1	0.426253	0.237662	77.92182	1.794	0.0768
sexm	-0.01717	0.152068	56.98653	-0.113	0.9105
age	-0.01234	0.006266	59.78532	-1.97	0.0535
wg_groupsizemedium	-0.08199	0.419868	37.52872	-0.195	0.8462
wg_groupsizesmall	0.020522	0.472041	74.69907	0.043	0.9654
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	4.480677	0.751444	23.50768	5.963	4.06E-06
relativesrel	-0.17104	0.256722	63.02319	-0.666	0.508
sexm	0.09276	0.176342	42.53099	0.526	0.602
age	-0.01275	0.008065	30.04699	-1.581	0.124
wg_groupsizemedium	-0.23873	0.706715	21.34317	-0.338	0.739
wg_groupsizesmall	-0.29204	0.827331	21.48113	-0.353	0.728

Table 17. The linear model results for hematocrit. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	34.15659	2.18181	15.655	<2e-16
solitary1	0.64611	1.32738	0.487	0.628
sexm	0.17313	1.01961	0.17	0.866
age	0.05195	0.03331	1.56	0.123
wg_groupsizemedium	-0.25873	1.97078	-0.131	0.896
wg_groupsizesmall	-0.25852	2.50334	-0.103	0.918
b	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	31.38385	3.414	9.193	2.61E-13
relativesrel	0.93442	1.45456	0.642	0.5229
sexm	0.10046	1.1476	0.088	0.9305
age	0.07737	0.03859	2.005	0.0492
wg_groupsizemedium	1.99849	3.20897	0.623	0.5356
wg_groupsizesmall	1.95276	3.69039	0.529	0.5985

Table 18. The linear model results for heterophil/lymphocyte ratio. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	0.941914	0.133635	45.56502	7.048	8.10E-09
solitary1	0.197807	0.16465	62.77956	1.201	0.234
sexm	-0.08830	0.127956	67.73502	-0.69	0.493
age	0.002321	0.004144	50.66945	0.56	0.578
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	9.35E-01	1.35E-01	3.61E+01	6.919	4.12E-08
relativesrel	9.19E-03	1.31E-01	6.39E+01	0.07	0.944
sexm	2.05E-03	1.27E-01	5.78E+01	0.016	0.987
age	7.06E-04	4.19E-03	3.35E+01	0.168	0.867

Table 19. The linear model results for triglycerides. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	6.89698	7.33814	48.31297	0.94	0.352
solitary1	-3.40544	4.03798	78.78622	-0.843	0.402
sexm	-1.89316	2.44967	59.10654	-0.773	0.443
age	0.08231	0.10673	64.93798	0.771	0.443
wg_groupsizemedium	1.44707	6.97942	38.4342	0.207	0.837
wg_groupsizesmall	3.22747	8.05397	76.06111	0.401	0.69
b	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**
(Intercept)	10.05455	12.06675	28.68623	0.833	0.412
relativesrel	-2.28161	3.78105	62.46057	-0.603	0.548
sexm	-2.76676	2.79856	47.96103	-0.989	0.328
age	-0.02741	0.13741	34.82224	-0.199	0.843
wg_groupsizemedium	0.95003	11.46802	27.38071	0.083	0.935
wg_groupsizesmall	5.84914	13.7989	24.69001	0.424	0.675

Table 20. The linear model results for total white blood cells. a) The linear model run with solitary. b) The linear model run with relatives.

a	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	18991.11	1786.53	10.63	< 2e-16
solitary1	71.85	1028.73	0.07	0.94449
sexm	260	846.28	0.307	0.75944
age	-72.71	26.03	-2.794	0.00647
wg_groupsizemedium	-2221.51	1611.62	-1.378	0.17178
wg_groupsizesmall	-1248.68	2048.16	-0.61	0.54375
b	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	19197.76	3032.5	6.331	2.89E-08
relativesrel	-665.91	1289.97	-0.516	0.6075
sexm	-385.58	1041.29	-0.37	0.7124
age	-81.91	32.28	-2.537	0.0137
wg_groupsizemedium	-1830.58	2781.74	-0.658	0.5129
wg_groupsizesmall	-1501.87	3222.52	-0.466	0.6428