Is there a link between allomothering and personality? Insights from a population of semi-captive Asian elephants (*Elephas maximus*) working in Myanmar's timber industry

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Abstract

Allomothering is a common behavior observed in many long-lived social species, including elephants. However, the underlying factors driving allomothering behavior remain unclear. This study investigates the link between allomothering and personality in a population of semi-captive Asian elephants working in Myanmar's timber industry and aims to confirm the repeatability of allomothering behavior in this population. Data was collected from 2014 to 2018 via questionnaires directed at elephant keepers. A repeatability analysis was conducted to determine the repeatability of allomothering behavior. To investigate the link between allomothering and personality, a combination of measurement invariance analysis and generalized linear mixed models were employed. My study found that allomothering is a repeatable behavior, but the available data did not provide support for a link between allomothering and personality. Interestingly, my study suggests that captive-born elephants are more likely to exhibit allomothering behavior than wild-caught elephants. This research sheds light on allomothering behavior in Asian elephants, which can be valuable for improving the management and welfare of captive elephants.

Keywords*: Allomarental care, temperament, cooperation, semi-captive, questionnaire data, measurement invariance, repeatability.*

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1. Introduction

Research into cooperative social behavior is essential for understanding of the ecology and evolution of group-living species, informing conservation and management efforts of endangered species, developing effective intervention strategies for captive animals, and gaining insight into our own behavior as a social species. Affiliative social relationships between group members contribute strongly to overall group cohesion and stability, and therefore welfare (Cameron et al., 2018; McCowan et al., 2008; Shimada & Sueur, 2014; Williams et al., 2018). Affiliative social bonds are widely present among animals and involve relationships with parents, offspring, siblings, mates, and non-related members of the same species (Massen et al., 2010; Silk, 2007) . Allomothering - the act of an individual caring for another individual's offspring - is an intriguing affiliative behavior observed in numerous social species including primates (Tecot & Baden, 2015), elephants (Lee, 1987; Schulte, 2000), cetaceans (Mann et al., 1998), canids (Pal et al., 2021), equines (Cameron et al., 2018) and rodents (Schubert et al., 2009); suggesting that relatively strong selective pressures helped shape this behavior early in evolution. However, the underlying factors contributing to the maintenance of allomothering remain unclear.

Allomothering can have both positive and negative fitness effects for mothers, allomothers, and offspring (reviewed Rosenbaum & Gettler, 2018a, 2018b; primates, Tecot & Baden, 2015). For instance, if an allomother provides direct care to a mother's offspring, the mother can benefit from increased time for foraging, while the allomother can improve its ability to care for young (Fairbanks, 1990), and offspring benefit from additional care. Moreover, the additional care provided by allomothers can increase the mothers birth rates and offspring survival rates (Fairbanks, 1990; Lahdenperä et al., 2016). However, if an allomother is not cautious enough, the offspring may become more vulnerable, and the mother may risk losing her offspring. Overall, the fitness benefits and consequences of allomothering can vary depending on the social structure of the species (for example, kinship, social rank, and age of group members) and various environmental factors such as resource availability (O'brien & Robinson, 1991). Providing care as an allomother is, however, an expenditure of both time and energy, and this is particularly noteworthy when the offspring in question does not appear to be directly related to the allomother.

An individual's consistent behavioral patterns (i.e., animal personality/temperament; Réale et al., 2007) can influence the selection of their social companions and overall social behavior (Harcourt et al., 2009; Pike et al., 2008; Schürch et al., 2010; Schürch & Heg, 2010a, 2010b; Webster et al., 2009; Wolf et al., 2007). For instance, infant temperament has proven to affect the development of social relationships in primates (Weinstein 2008). In humans, parenting style is influenced by personality (Huver et al., 2010). In cooperatively breeding cichlids, variation in behavioral types is linked to variation in cooperation, the extent of group-living, and reproductive decisions (Schürch & Heg, 2010). The association between animal personality and group stability, cooperative conduct, and even parenting style suggests a possible association between personality and allomothering. For example, one can speculate that if an individual's personality makes it more aggressive this will make it less likely to provide allomothering services or more likely to openly reject young individuals. Research into the relationship between allomothering and personality can provide valuable insight into the evolutionary processes behind the development of temperaments, as well as the factors that make certain temperaments flourish in specific environments. This knowledge is especially valuable for the practical implementation of conservation efforts and improving captive animal welfare.

Asian elephants (*Elephas maximus*) are an endangered species (IUCN, 2022) with a complex cooperative social structure where individuals engage in allomothering behavior (Schulte, 2000). Females play a dominant role in allomothering behavior, and their matriarchal society allows for a better understanding of cooperation in group-living species. Additionally, the long lifespan of Asian elephants allows for the study of allomothering behavior over an extended period of time, providing valuable insights into how this behavior changes and evolves over an individual's lifespan. These characteristics make Asian elephants a valuable species for studying the link between allomothering and personality. Furthermore, as allomothering can significantly improve individual fitness in Asian elephants and captured elephants suffer from long-term reduced birth rates, understanding their allomothering behavior can be especially useful for their conservation, which is vital for the long-term survival of the species (Jackson et al., 2019; Lahdenperä et al., 2016, 2018, 2019).

Interestingly, in African elephants (*Loxodonta africana*), allomothers had the lowest rate of initiating aggression towards calves (Lee, 1987). Most interactions were affiliative, in contrast to for example primates (Silk, 1980). One would expect to find that more sociable female Asian elephants will tend to provide allomothering care, while more aggressive females would be less inclined to do so. This is because sociable individuals are more likely to interact positively with members of the group (Williams et al., 2019b), while more aggressive individuals might be more volatile and moodier providing less opportunity for the establishment of healthy stable social bonds.

I researched the link between allomothering behavior and personality in a population of semi-captive Asian elephants working in Myanmar’s timber industry. I used behavioral data collected from questionnaires directed at elephant handlers over a period of four years (2014 – 2018). First, I investigated the repeatability of allomothering behavior. Repeatability focuses on the consistency of an animal's behavior over time and across different environments and is crucial for determining individual differences in behavior. After assessing the repeatability of allomothering, I then examined the potential association between allomothering and personality. The personality structure of this population was previously summarized into three main personality factors: Attentiveness, Sociability, and Aggressiveness (Seltmann et al., 2018). I hypothesized that allomothering would be a consistent behavior and that more sociable females would be more likely to engage in allomothering, while more aggressive females would be less likely to engage in allomothering.

2. Methods

All methods were performed in accordance with relevant guidelines and regulations established by the corresponding national governmental authorities and the ethical board of the University of Turku.

Study population

I studied a population of semi-captive Asian elephants owned by the Myanma Timber Enterprise (MTE), a governmental institution supervised by the Myanmar Ministry of Natural Resources and Environmental Conservation (MONREC). The MTE oversees approximately 3,000 semi-captive Asian elephants distributed in forest camps across the country (**Figure 1a**). The Myanmar government regulates the working hours and tonnage of each elephant depending on its age, sex, reproductive status, and the working season. Elephants are assigned to work in small groups of on average 6 elephants (range: 4 – 12 elephants). During the day, elephants work as transport and draft animals. At night, the elephants are free to forage in the surrounding forest where they may interact with other semi-captive or wild conspecifics. In the early stages of the training process – beginning at the age of 5 or at the age of capture – each elephant is assigned an elephant-handler called an *oozie* (**Figure 1b**). The oozie guides the elephant's work and is responsible for retrieving his elephant from the forest every morning and providing daily care such as, bathing and monitoring of welfare, diet, defecation, and sleeping habits for his elephant (Crawley et al., 2019; Mumby, 2019). The elephants begin to fully work in the timber industry at the age of 17 after completing the training program and retire at the age of 55. Further details on the demography and life history of the Myanmar timber elephants are provided in Mar (2007) and references therein. I obtained life-history data of elephants as well as each elephant's oozie's age and years of experience with their focal elephant from logbooks provided by the MTE that are updated monthly by local MTE veterinarians (**Figure 1c**).

Figure 1. Study population and data collection. A. Myanmar states divisions and study townships. Study state in green. Study regions pinned in red. B. Oozie guiding an Asian elephant working for the Myanmar Timber Enterprise (MTE). C. MTE logbooks. D. Questionnaire data collection.

Data collection: questionnaires

I used previously collected behavioral data gathered from questionnaires directed at oozies (Lynsdale et al., 2022; Seltmann et al., 2018, 2019, 2022). Subjective assessments of animal behavior conducted by experienced observers/caregivers allows for information to be gathered in a reliable, time- and cost-efficient manner and can be especially useful when other methods - such as behavioral coding or experimental observations - are not feasible (Barnard et al., 2016; Carter et al., 2012; Ijichi et al., 2013; Tetley & O'Hara, 2012; Uher & Asendorpf, 2008). Otherwise known as *rater-coding*, subjective assessments of animal behavior occur when an observer rates the behavior of a focal individual, indicating whether a behavior is present or absent, or rating the intensity of a particular behavior. Observations were collected via questionnaires directed at the oozies because they work closely with elephants daily and therefore develop an in-depth knowledge of their elephant's behavioral tendencies and social interactions. I used the focal elephant oozie's rating and that of the head oozie whenever possible to ensure that raters had sufficient exposure to the focal elephant. Oozies were instructed not to discuss their ratings with each other to ensure the independence of assessments. Colleagues from Myanmar - who have extensive experience working with elephants and are well acquainted with the English language - translated the questionnaires from English to the oozies native language of Burmese (**Figure 1d**). The questionnaires were then back translated from Burmese to English to ensure the accuracy of the intended questions. The observations reported by oozies should therefore represent a reliable, comprehensive overview of elephant behavior under semi-captive conditions.

Allomothering questionnaire data

Allomothering behavior data was collected between 2014 and 2018 during the dry season (i.e., mid-February to mid-May). Allomothering status was determined by asking oozies if they had seen the focal individual taking care of another female's calf during work or free time. Oozies would then provide the MTE ID number of the mother, calve, and allomother. In addition to allomothering status, oozies were asked what type of activities allomothers performed with calves (e.g., resting, playing, or protecting), how frequently allomothers were seen with calves ('Nearly always', 'Often', 'Sometimes'), and if the same allomothers cared for the same female's calves before. The complete social questionnaire used to gather allomothering data is appended in **Supplementary material 2**.

Personality questionnaire data

The personality structure of my study population was previously assessed using factor analysis (Seltmann et. al., 2018). Personality data was collected between 2014 and 2018 during the dry season (i.e., mid-February to mid-May) and, only for the year 2018, during the wet season (i.e., mid-May to late October). Questionnaires were designed using a combination of top-down and bottom-up approaches as described in Seltmann et. al. (2018) and references therein. Elephant personality in my study population can be represented by three factors: 'Attentiveness', 'Sociability', and 'Aggressiveness' (Seltmann et. al., 2018). Two oozies rated the frequency of behavioral items on a 4-point scale, with 1 meaning 'Very rarely', 2 'Occasionally', 3 'Quite a lot', and 4 'Most of the time'. **Figure 2** shows the resulting factor model, with 15 behavioral items loading on the three personality factors.

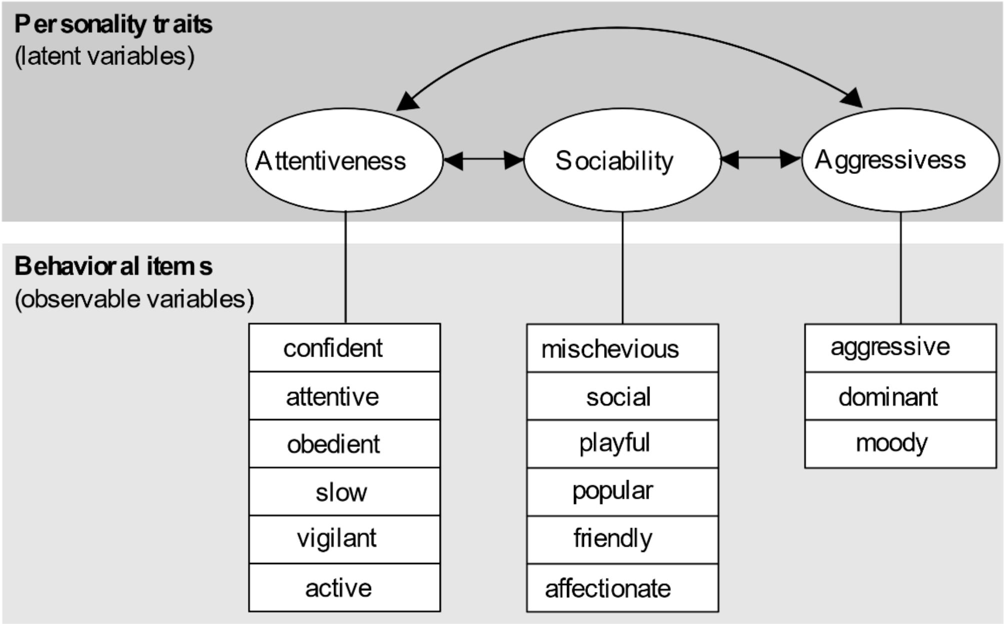

Figure 2. Personality structure of semi-captive Asian elephants of the Myanmar Timber Enterprise. Bidirectional arrows denote covariance between the personality factors (latent variables). Connections denote direct effects (regressions) of the personality traits onto the behavioral items (observed variables).

Focal individuals

My study centered on mature female elephants over the age of 17 that completed their training period and have been incorporated into workgroups. Workgroups without calves were excluded from analysis because these likely do not provide many opportunities for allomothering relationships to develop. One elephant in the dataset under 17 years of age (13 years old) was reported performing allomothering behaviors, this elephant was excluded from analysis because it was still undergoing training. I then excluded elephants for which I did not have sufficient data available on personality or allomothering behavior. **Table 1** summarizes the sample available for the analysis of the repeatability of allomothering behavior and the sample available for the analysis of the link between allomothering behavior and personality. A complete overview of the descriptive statistics and visual data exploration performed are provided in **Supplementary material 1**.

Table 1. Study sample summary. Descriptive statistics of samples available for the analysis of the repeatability of allomothering behavior and for the analysis of the link between allomothering behavior and personality.

	Study sample for the repeatability analysis of allomothering behavior	***Study sample for the analysis of the link between allomothering and personality***
Total number of observations	107	34
Total number of elephants	69	26
Median age of elephants in years (range)	34 (17 - 59)	38 (17 - 57)
Total number of allomothers (observations)	29 (47)	9 (14)
Total number of non-allomothers (observations)	40 (60)	17 (20)
Median age of allomothers in years (range)	31 (21 - 56)	25 (19 - 53)
Median age of non-allomothers in years (range)	38 (17 - 59)	45 (17 - 57)
Total number of captive-born elephants	51	18
Total number of wild-caught elephants	18	8
Median age of captive-born elephants in years (range)	28 (17 – 59)	26 (17 – 57)
Median age of wild-caught elephants in years (range)	51 (40 – 57)	51 (44 – 55)
Median years of experience of oozies (range)	1 (0.8 – 9)	1 (0.8 – 9)
Median age of oozies in years (range)	23 (15 – 55)	23 (15 – 55)
Calf sex	16 male calves, 12 female calves, and 41 calves of unreported sex	6 male calves, 3 female calves, and 17 calves of unreported sex
Regions	18 elephants from Katha and 51 elephants from Kawlin	6 elephants from Katha and 20 elephants from Kawlin
Number of workgroups	34	20
Percentage of workgroups with 1 calve available	~60%	~75%

Statistical analysis

All statistical analysis were conducted in R v. 4.2.1 (R Core Team 2022).

Repeatability analysis of allomothering behavior

I estimated the repeatability of allomothering status within a generalized linear mixed modelling framework (following Nakagawa & Schielzeth, 2010), using the R package *rptR* (Stoffel et al., 2017). GLMM-based repeatability estimation requires a model to be specified, I specified a model following four steps: (a) variable selection, (b) variable assessment, (c) model specification, and (d) model assessment. I first selected potential confounding variables from the data available (**Table 2**).

Table 2. Variable selection. A list of potential confounding variables and the corresponding reasoning for their consideration in model selection for GLMM-based repeatability analysis.

	Variable of interest	*Reasoning*
Categorical variables	**Origin**: If the focal elephant is wild-caught (W) or captive-born (C)	The conditions (environment, social environment, resource availability, etc.) under which an elephant is raised - and the experience of being captured itself - may affect an individual's long-term stress levels, quality of life, and behavior (Lahdenperä et al., 2018, 2019; Webber, 2017). Additionally, consistent human-animal relationships can introduce a variety of stressors that wild animals do not encounter (Crawley et al., 2021). Stress in turn can affect how an individual interacts with conspecifics.
	Region: Location where the questionnaire was conducted	The different regions in which questionnaires were conducted may be inherently different from each other in terms of general oozie-elephant relationships, social lifestyle, environmental inputs, working conditions, and resource availability.
	Social status: High, average, low in comparison to the other members of the workgroup	Social status affects power dynamics within social groups. Females of lower social status may be more inclined to provide allomothering services to females of higher social status (Fairbanks, 1990). Additionally, dominant females within elephant groups are also usually older females which are more prone to provide allomothering care (Lahdenperä et al., 2016 and references therein).
Continuous variables	**Age**: The age of the focal elephant at the time of the questionnaire	Allomothering offers different trade-offs at different life stages. For example, young females who participate in allomothering may gain experience that can help them become better mothers themselves. Older females may benefit from caring for closely related grand-calves. However, the energy and time investment may have disparate consequences for different age groups, so females of a certain age may be more likely than others to invest their time in allomothering (Blell, 2018; Lahdenperä et al., 2016).
	Oozie experience: The years of experience of the respondent with the focal elephant.	Animal handlers with more experience with a particular elephants can provide more consistent reliable observations and more experienced handlers agree that experience is a key aspect of handler-elephant relationship (Crawley et al., 2021; Jolivald et al., 2022; Mumby, 2019).
	Oozie age: The age of the questionnaire respondent.	Changes have occurred recently within the oozie profession across Asia, with oozies tending to be younger and less experienced (Crawley et al., 2019, 2021), having fewer employment options, and exhibiting higher job turnover than in the past (Srinivasaiah et al., 2014). Younger oozies are less experienced and may not be as perceptive as older oozies.

After selecting potential confounding variables, I then individually assessed the association between the untransformed variables and allomothering status (allomother/non-allomother). I assessed the association between potential confounding categorical variables and allomothering status using Fisher's exact test. Fisher's exact test for count data is a non-parametric method for comparing the proportion of categories in two different independent groups in a contingency table. Fisher's exact test is most used to analyze a 2x2 contingency table, but it can also be used to analyze data from a larger contingency table (for example, a 3x2 contingency table). Fisher's exact test assumes (1) the two variables are categorical and data is randomly sampled (2) the levels of variables are mutually exclusive (3) observations are independent of each other (4) observation data are frequency counts and not percentages, proportions or transformed data. My categorical variables met most of Fisher's exact test assumptions. My sample, however, includes some instances of repeated measures (violation of assumption 3); I proceed with my exploratory analysis as indicated and account for non-independence of observations in further statistical analysis. Unlike the chi-square test, the Fisher's exact test is an exact test (i.e., returns exact p-value) and can be applied to small sample sizes. This test is an alternative to the chi-square test, especially when the frequency count is < 5 for more than 20% of cells. **Table 3** shows the results of the categorical variable assessment step.

I used a binary logistic regression to individually assess the association between 3 continuous predictor variables - elephant age, oozie age, and oozie experience - and allomothering status. Binary logistic regressions require that (1) the dependent variable is discrete and dichotomous in nature (2) there should be no extreme outliers (influential values) in the data, (3) there should be no high intercorrelations (multicollinearity) among predictors, and (4) there is a linear relationship between the logit of the outcome and each predictor variables. Neither elephant age, nor oozie age met the assumption of a linear relationship between the logit of the outcome and the predictor variable. Therefore, I incorporated spline functions into my tests. Spline functions fit a smooth curve with a series of polynomial segments to appropriately assess the relationship between a potential predictor variable and an outcome variable. The results of the continuous variable assessment step are shown in **Table 4**.

Following the variable assessment step, I built a global model including origin and oozie experience from which I could potentially extract a simpler model to fit the data. I identified the possible predictors of allomothering status using a backward stepwise selection procedure. At each step, variables were removed based on p-values, removing the variables with the largest (less significant) p-values at each step. I used Akaike's information criterion corrected it for small sample size (AICc) as my predefined stopping rule. As shown in **Table 5**, the model reporting the smallest AICc value included both elephant origin, oozie experience, and oozie age. However, oozie age did not meet the linearity assumption of the binary logistic regression and adding splines into my final analysis made the model overly complex for the small sample size. This was demonstrated by a lack of convergence when attempting to run the repeatability analysis. I therefore excluded this variable from further analysis. The final model included allomothering status as the dependent variable**,** origin and oozie experience as fixed effects, and elephant ID as a random effect (i.e., grouping factor). I used likelihood ratio tests (applying the `anova()` function in R) to assess the goodness-of-fit between the selected model against a simpler nested model which only included elephant origin; the model including elephant origin and oozie experience fit the data significantly better (**Table 6**).

Once I selected a model for GLMM-based repeatability estimation, I estimated the adjusted repeatability (an approach which adjusts for confounding factors, see Nakagawa & Schielzeth, 2010) of allomothering behavior. I fitted the model with a binomial distribution (allomother: allomother/non-allomother) and used a logit link for binary data as advised by Stoffel et al., (2017). *rptR* relies on an additive overdispersion model to estimate repeatability. Confidence intervals (95%) were obtained by parametric bootstrapping (n= 1,000 loops). P-values for the repeatability estimate were calculated with likelihood ratio tests. Repeatability values range from 0-1 with values ranging from 0.5-0.7 indicating moderate repeatability and values greater than 0.7 indicating high repeatability (Harper, 1994).

Linking allomothering behavior to animal personality

To investigate the link between allomothering and personality, I aimed to compare the average personality factor scores (i.e., attentiveness, sociability, and aggressiveness) and their variances and covariances between allomothers and non-allomothers. To make valid comparisons of latent personality factors between allomothers and non-allomothers, I verified (1) if the previously established personality factor model (Seltmann et al., 2018) fit my sample well enough and (2) if there is measurement invariance between allomothers and non-allomothers. All item scores were treated as continuous variables (following Seltmann et al., 2018). Factor loadings and intercepts were constrained to have average values of 1 and 0 respectively, following an effects-coding method. Factor means can therefore be interpreted as optimally weighted averages of their items and variances as the average amount of an item’s variance explained by a personality trait (following Seltmann et al., 2019). All analysis of the link between allomothering and personality was conducted using the lavaan package in R (Rosseel, 2012).

I performed an unconstrained confirmatory factor analysis (CFA) to examine the fit of the previously established personality factor model (Seltmann et. al., 2018) to my sample. Model fit was assessed using four separate fit indices. The root mean square error of approximation (RMSEA) and the standardized root mean square residual (SRMR) are badness-of-fit measures (i.e., 0 indicates a perfect fit of the model). The comparative fit index (CFI) and the Tucker-Lewis Index (TLI) are goodness-of-fit measures (i.e., a value closer to 1 indicates a good fit of the model). RMSEA has the added benefit of providing 90% confidence intervals for the estimate and it can be used to test the null hypothesis that the estimate is <0.05, indicating a good fit. The rough cut-off value used to indicate a well-fitting model for SRMR, and CFI was > 0.95. The results of this analysis are shown in **Table 7**. My initial sample seemed to be too small to conduct a measurement invariance analysis, I therefore expanded my sampling to include all females over the age of 18 (n = 254) and proceeded with the intended analysis (details in results section).

I then conducted a measurement invariance analysis to verify that the interpretations of the personality factors being inferred from questionnaire item scores are consistent across allomothers and non-allomothers (following Seltmann et al., 2019 and references therein). To test for measurement invariance, I estimated and compared increasingly constrained CFA models with each other (a method known as multi-group confirmatory factor analysis). The first model is a configural invariance model, which is an unconstrained model where factor loadings, intercepts, and residual variances are free across groups and only the factor structure is the same among groups. This model allows us to test whether the same factor structure holds across allomothers and non-allomothers. After examining configural invariance, I examined the metric and scalar invariances. Metric invariance is a constrained version of the configural model where the factor loadings are assumed to be equal across groups and the intercepts are allowed to vary between groups. Metric invariance enables the comparison of factor variances and covariances between the groups. Scalar invariance in turn is a constrained version of the metric invariance model where both the factor loadings and intercepts are assumed to be equal across groups. Scalar invariance allows the comparison of factor means between the groups. Measurement invariance was tested using a chi-square difference test. If measurement invariance is given (i.e., there are no significant differences between models), I would proceed the analysis by comparing personality factor means, variances and covariances. However, I did not find evidence of measurement invariance between allomother and non-allomothers (see results; **Table 8**).

The lack of measurement invariance indicates that that the latent constructs cannot be measured and interpreted in the same way across groups and the comparisons might be confounded by measurement quality across the groups. Hence, to investigate the link between allomothering and personality, I decided to instead compare observed measures (i.e., item scores) between allomothers and non-allomothers. For this, I performed a series of generalized linear mixed models (GLMMs) using the 15 behavioral items scored using my initial sample (n=34) (see behavioral items in **Figure 2**). I used mean items scores per measurement occasion. Models accounted for elephant ID as a random effect, the explanatory variable of interest as a fixed effect, and allomothering status (allomother/non-allomother) as the dependent variable. Given the small sample size, I did not add additional explanatory variables such as elephant origin or oozie experience. I used a Bonferroni corrected alpha to assess the significance of associations.

3. Results

Repeatability analysis of allomothering behavior

Model selection for GLMM-based repeatability estimation

Of the categorical variables considered, elephant origin was associated with allomothering status in year 2015, as indicated by the significant p-value obtained from Fisher's exact test for year 2015 [**Table 3**; **p-value (two-tailed) = 0.0353**, Odds ratio = 0.168, 95% CI = 0.0152- 1.00]. The odds ratio (OR) can be used as an effect size for understanding the effect of elephant origin on allomothering status. A value of OR >1 indicates increased occurrence of an event, while OR <1 indicates decreased occurrence of an event. The odds of an elephant being an allomother in the wild-caught group are 0.167 times the odds of an elephant being an allomother in the captive-born group. The odds ratio of 0.167 therefore indicates that captive-born elephants are more likely to exhibit allomothering behavior than wild-caught elephants. There was no significant association between allomothering status and origin for any other year. **Figure 3** shows the frequency counts of allomothers and non-allomothers by elephant origin for the year 2015.

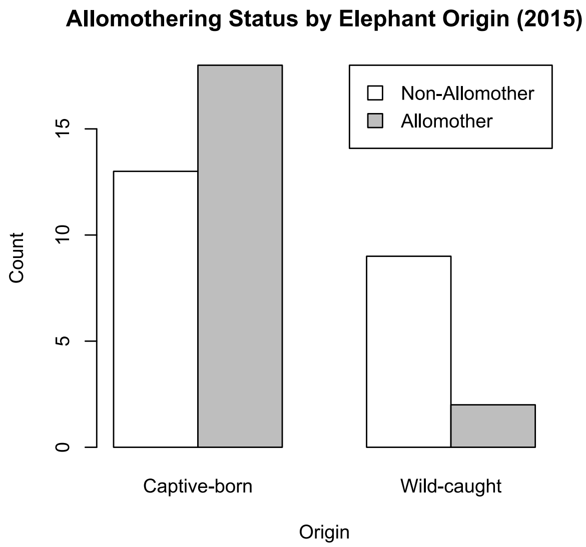

Figure 3. Allomothering status by elephant origin for the year 2015. Frequency counts of allomothers and non-allomothers by elephant origin for the year 2015.

I did not find any significant association between allomothering status and region, nor between allomothering status and social status for any year (**Table 3**). For some years, the variable assessment for both region and social status lacked enough categories for comparison, therefore these variables were not considered in further analysis. In summary, of the categorical variables examined, I considered including only elephant origin into the final model.

Table 3. Categorical variable assessment. Assessment of the association between potential confounding categorical variables and allomothering status. 0 = non-allomother; 1=allomother; C = captive-born; W = wild-caught.

Variable	*year*	*Contingency table*			*p-value (Two-tailed)*	*Odds-ratio*	*95% CI*
Origin	**2014**		**C**	**W**	1	0.694	0.00851 - 20.3
		0	4	2			
		1	3	1			
	2015		**C**	**W**	**0.03532***	0.168	0.0152 - 1.00
		0	13	9			
		1	18	2			
	2016		**C**	**W**	1	0	0.00 - 58.4
		0	2	2			
		1	1	0			
	2017		**C**	**W**	1	0	0.00 - 117
		0	2	1			
		1	1	0			
	2018 early		**C**	**W**	1	0.794	0.0572 - 7.45
		0	11	4			
		1	7	2			
	2018 late		**C**	**W**	0.1373	0	0.00 - 3.22
		0	5	2			
		1	11	0			

Region	**2014**		**Katha**	**Kawlin**		0.5	4.17	0.141 - 351
		0	5	1				
		1	2	2				
	2015		**Kawlin**	**West Katha**		0.08663	6.71	0.654 - 346
		0	21	1				
		1	15	5				
	2016		**Kawlin**			NA	NA	NA
		0	4					
		1	1					
	2017		**Kawlin**			NA	NA	NA
		0	3					
		1	1					
	2018 early		**East Katha**	**Kawlin**	**West Katha**	0.8107	NA	NA
		0	3	10	2			
		1	2	7	0			
	2018 late		**Kawlin**	**West Katha**		0.3889	0	0.00 - 24.8
		0	6	1				
		1	11	0				
Social status	**2014**		**Average**	**High**	**Low**	0.7143	NA	NA
		0	3	2	1			
		1	2	2	0			
	2015		**Average**	**High**	**Low**	0.513	NA	NA
		0	17	4	1			
		1	15	2	3			
	2016		**Average**	**High**		1	0	0.00 - 58.4
		0	2	2				
		1	1	0				
	2017		**Average**			NA	NA	NA
		0	2					
		1	1					
	2018 early		**Average**			NA	NA	NA
		0	11					
		1	8					
	2018 late		**Average**	**High**	**Low**	0.7169	NA	NA
		0	5	2	0			
		1	9	1	1			

I performed binary logistic regressions to assess the relationship between allomothering status and various continuous variables. Variables that violated the linearity assumption of the logistic regression were modeled using natural splines. I did not find a significant association between any of the potential continuous predictor variables considered and allomothering status (**Table 4**). I found no statistically significant reason for including any of the variables considered into the final model. However, both oozie experience and age seem to be somewhat associated with allomothering status albeit the association is not significant. In summary, of the continuous variables assessed, I considered including oozie age and experience into the final model.

Table 4. Continuous variable assessment. Association between various continuous predictor variables and allomothering status of elephants as assessed via logistic regression. Both elephant age and oozie age were assessed using natural splines (indicated by ns; ns = natural splines) and corresponding degrees of freedom.

Variable	*Log odds (Estimate)*	*Standard error*	*z-value*	*p-value*	*AIC*
Elephant age					152.57
ns (age, df = 6)1	0.8141	1.3005	0.626	0.531	
ns (age, df = 6)2	1.8998	1.8039	1.053	0.292	
ns (age, df = 6)3	1.2784	1.6051	0.796	0.426	
ns (age, df = 6)4	-0.8355	1.4191	-0.589	0.556	
ns (age, df = 6)5	1.6705	2.8888	0.578	0.563	
ns (age, df = 6)6	-0.8168	1.3396	-0.610	0.542	
Oozie age					154.5
ns (oozie age, df = 6)1	2.27992	1.22719	1.858	**0.0632·**	
ns (oozie age, df = 6)2	-1.77391	1.51790	-1.169	0.2425	
ns (oozie age, df = 6)3	1.27517	1.36696	0.933	0.3509	
ns (oozie age, df = 6)4	0.06073	1.34446	0.045	0.9640	
ns (oozie age, df = 6)5	-0.26038	2.37913	-0.109	0.9129	
ns (oozie age, df = 6)6	1.34690	1.31962	1.021	0.3074	
Oozie experience					146.22
oozie experience	-0.21220	0.12419	-1.709	**0.0875·**	

After I selected potential confounding variables, I constructed a global model which included elephant origin, oozie experience, and oozie age and selected a final model using a backwards stepwise selection procedure, using AICc as a predefined stopping rule. The model with the lowest AICc value included elephant origin, oozie experience, and oozie age as fixed effects. This model however did not converge during the repeatability analysis. Oozie age may create an overly complex model for my sample. I therefore used the nested model with the second lowest AICc value, which included only elephant origin and oozie experience as fixed effects (**Table 5**).

Table 5. Model specification. Selected predictors and model fit as determined by the AICc.

Predictors	*AICc*
Elephant origin, oozie experience, and oozie age	116.7016
Elephant origin and oozie experience	134.6354
Elephant origin	136.9548

Given my small sample size, I considered whether using a simpler model including only elephant origin as a confounding variable. I verified model fit to the data by comparing the selected model to the simpler model. The model selected using the AICc criterion included elephant origin and oozie experience as fixed effects. This model fit the data significantly (p-value < 0.05) better than the simpler model which only included elephant origin (**Table 6**).

Table 6. Model assessment.

Predictors	*Df*	*AIC*	*BIC*	*logLik*	*Deviance*	*Chisq*	*Chi Df*	*p-value (>Chisq)*
Elephant origin and oozie experience	4	134.24	144.89	-63.120	126.239	4.4801	1	**0.03429**
Elephant origin	3	136.72	144.71	-65.36	130.72			

Repeatability estimation

I calculated the adjusted repeatability accounting for the effects of both origin and oozie experience. Allomothering was repeatable across the four-year study (n = 106 observations corresponding to 69 study subjects; link-scale: R [95% CI] = 0.676 [0.114, 0.995]; p-value (permutation) = 0.001; original-scale R [95% CI] = 1.441 [0.121, 183.045]; p-value (permutation) = 0.001).

Linking animal personality to allomothering behavior

To investigate the association between allomothering and personality I first verified if the previously established factor model fit my data well. I then performed a measurement invariance analysis using a multigroup confirmatory factor analysis approach. After finding a lack of measurement invariance I performed a series of generalized linear mixed models using behavioral items scores as fixed effects.

The previous model seemed to fit the study sample well enough (**Table 7**). I then proceeded to perform the measurement invariance analysis. However, this sample was too small (n=34) to run through the measurement invariance analysis which resulted in a sample covariance matrix that was not positive-definite. I then performed the measurement invariance analysis using a larger sample (n=254) which included all females above the age of 18 across the four year-study. After confirming appropriate model fit of the personality factors to the larger sample (**Table 7**), I proceeded to examine measurement invariance by testing configural, metric, and scalar invariance.

Table 7. Assessment of previously established personality factor model fit to my sample.

Fit measure	*Threshold*	*Study sample (n=34)*	*Expanded sample (n=254)*
The comparative fit index (CFI)	> 0.95	0.962	0.973
Tucker-Lewis Index (TLI)	> 0.95	0.955	0.967
Root mean square error of approximation (RMSEA)	< 0.05	0.096	0.065
Standardized root mean square residual (SRMR)	< 0.05	0.054	0.034

I performed a chi-square difference test to assess measurement invariance between the three models. I did not find evidence of measurement invariance as indicated by the significant differences between the three models (**Table 8**).

Table 8. Measurement invariance assessment.

Model	*χ2*	*Δχ2*	*df*	*Δdf*	*p-value (χ2)*
Configural	321.20		174		
Metric	348.37	27.168	186	12	**0.0073080**
Scalar	382.18	33.812	198	12	**0.0007221**

The lack of measurement invariance indicates that the comparison of latent personality factors would be inappropriate between allomothers and non-allomothers. I thus proceeded to run GLMMs on observed item scores instead, as previously described. I used a Bonferroni corrected p-value to counteract increased type I error. This Bonferroni corrected p value is (0.05/15) ~0.003. I did not find a significant association between the behavioral items considered and allomothering status (**Table 9**).

Table 9. Generalized linear mixed models results for the association between various behavioral items and allomothering status.

Relevant personality factor	*Explanatory variable*	*Estimate*	*Standard error*	*z value*	*p-value (>|z|)*
Sociability	Mischievous	0.07338	0.58617	0.125	0.900
	Social	0.9386	0.4796	1.957	0.0504
	Popular	0.3730	0.5527	0.675	0.500
	Friendly	0.5032	0.4311	1.167	0.2432
	Affectionate	0.6084	0.5857	1.039	0.299
	Playful	0.8571	0.5969	1.436	0.1510
Aggressiveness	Aggressive	0.1260	0.6701	0.188	0.851
	Dominant	-0.07467	0.74143	-0.101	0.920
	Moody	-0.9392	1.0099	-0.93	0.352
Attentiveness	Vigilant	-0.03662	0.48518	-0.076	0.940
	Slow	0.06093	0.44992	0.135	0.892
	Obedient	0.1003	0.5425	0.185	0.853
	Attentive	-0.1876	0.5620	-0.334	0.738
	Confident	0.1182	0.5080	0.233	0.816
	Active	0.5153	0.4988	1.033	0.302

4. Discussion

In this thesis, I investigated allomothering behavior in a population of semi-captive Asian elephants working in Myanmar's timber industry. I used behavioral questionnaire data collected over a period of four-years (2014-2018). I first aimed to establish the repeatability of allomothering behavior in this population. For this, I conducted a repeatability analysis and confirmed that allomothering is repeatable. My second aim was to examine the relationship between allomothering and personality. To do this, I employed a series of generalized linear mixed models (GLMMs) using personality-related behavioral items as fixed effects. Despite hypothesizing that more sociable females would exhibit a higher predisposition of allomothering, and more aggressive females to be less inclined to engage in this behavior, I could not find any significant association between allomothering and personality-related behaviors. A larger sample size is necessary to accurately evaluate the link between personality factors and allomothering behavior. In discussing the outcomes, I contextualize them within the study sample and provide recommendations for further inquiry and improved methodologies as well as consider the practical implications of the findings to captive animals.

Repeatability is a critical element of determining individual differences in behavior over time (Dingemanse & Wright, 2020; Réale et al., 2007). To my knowledge, this study is the first to explicitly assess the repeatability of allomothering behavior in Asian elephants. I found strong evidence to support that allomothering behavior is repeatable, indicating that certain individuals consistently provide allomothering care compared to others. This finding raises questions about the factors that influence an individual's inclination to provide allomothering services, and how this information can be applied to enhance our understanding of the evolution of cooperative behavior and – perhaps most importantly – improve the management strategies of Asian elephants in captivity.

Interestingly, I found that – at least for the year 2015 – captive-born elephants were more likely to exhibit allomothering behavior than wild-caught elephants. It has been found that zoo-housed Asian elephants engage in more affiliative interactions and fewer aggressive interactions when all members of a group are related to each other (Harvey et al., 2018). I hypothesize that perhaps related females are more likely to provide allomothering care and interact more frequently with the group overall. If wild-caught elephants are also less likely to be related to their assigned work group, this could explain why captive-born elephants are relatively more inclined to provide allomothering care than wild-caught elephants. Furthermore, wild-caught elephants suffer from higher increase of mortality when compared to captive-born elephants and are regarded by keepers as more difficult to train and having less reliable temperaments (Lahdenperä et al., 2018; Zaw, 1997). This suggests that elephants caught from the wild undergo stressful experiences that captive-born elephants may handle easier; the added stress could affect the ability of wild-caught elephants to engage in affiliative interactions, especially to care for and accept another female's offspring. Moreover, in zoo-housed Asian elephants, when individuals were related there were significantly more affiliative social interactions, but there was no relationship between the sociable personality component nor elephant origin, and affiliative social interactions (Williams et al., 2019a).

On the other hand, while it is important for herds to have related individuals, unrelated elephants can still form appropriate and successful social groupings with conspecifics (Williams et al., 2019a). Allomothering can be a way for unrelated individuals to effectively be incorporated into new groups because when calves are present the amount of affiliative behaviors between group members increases (Williams et al., 2019a). However, the condition and context under which a wild-caught or unrelated individual is introduced into a group could also influence the probability of it engaging in affiliative relationships with group members. For example, if an elephant – who was otherwise healthy and within a stable group - is captured and brought to a foreign environment this will most likely be a stressful experience that will hinder its ability to form affiliative relationships with new group members. Conversely, if an individual is found alone and vulnerable or in poor health, it might be more inclined to form part of a new group and establish affiliative social bonds. This is especially important to consider when moving animals in captive or semi-captive conditions as it can significantly improve or worsen welfare.

The social compatibility between group members in captive animals can significantly improve the likelihood of having positive social bonds that help maintain animal welfare (Meehan et al., 2016; Schmidt & Kappelhof, 2019; Williams et al., 2018). Affiliative social relationships between group members contribute to overall group cohesion and stability in elephants (Williams et al., 2018). Allomothering is a positive social interaction that significantly improves fitness by increasing calf survival and maternal birth rates (Gadgil & Nair, 1984; Lahdenperä et al., 2016; Prado-Oviedo et al., 2016; Schulte, 2000). I expected to find that more sociable females would be more likely to provide allomothering care, while more aggressive females would be less inclined to participate in this behavior. However, I did not find support for a link between allomothering and any of the behaviors related to personality factors. This goes in agreement with finding in zoo-housed elephants, where sociable personality components where not associated with affiliative behaviors (Williams et al., 2019a). It is important to note, however, that the statistical methods employed to examine the relationship between allomothering and personality in my study were not optimal due to limited sample size.

Firstly, I aimed to compare the means and covariance of the three latent personality factors between allomothers and non-allomothers. This required the verification of measurement invariance to ensure valid comparisons between groups using latent constructs such as personality factors (Meredith, 1993; Vandenberg, 2002). However, attempting to perform the analysis using my initial sample size produced an error where the sample covariance matrix is not positive-definite. The most likely reason for having a non-positive definite matrix is that the model includes too many variables and too few data, which can make the covariance matrix unstable. Another possibility is that I had multicollinearity in the matrix. Given my small sample size (**Table 1**) I believe the main problem was sample size.

Notably, after increasing my sample size to perform measurement invariance analysis, the fit of the personality factor improved, and my findings suggested that there is measurement non-invariance between allomothers and non-allomothers. Measurement non-invariance occurs when a construct has a distinct structure or interpretation across different groups. Consequently, the construct cannot be accurately tested or interpreted across groups or time periods. Although this apparent measurement non-invariance is most likely due to my limited sample size (increasing sample size improved the fit of the model), one way to further explore complex relationships between allomothering and personality is via path analysis. The main objective of path analysis is to test and estimate the direct and indirect relationships between variables in a hypothesized causal model (in this case, the personality factor model). Path analysis involves the use of structural equation modeling to estimate the strength and direction of relationships between variables by specifying a series of causal pathways. The goal is to test the overall fit of the model to the observed data and to determine the relative contributions of each variable to the outcome. This approach can provide insight into the factors affecting model fit and measurement non-invariance. However, small sample sizes would still be a limiting factor.

Secondly, I examined the association between behavioral items– which are the observed variables used to infer the latent personality factors – and allomothering. This is problematic because any single observed behavior likely does not accurately represent the entirety of the intended personality factor. This means that with the results available I am not able to properly assess the relationship between personality and allomothering, only the relationships between allomothering and the behavioral items observed. To this end, although none of the behaviors assessed were significantly associated with allomothering status, the social behavioral item seemed to have the strongest potential link to allomothering status. The social item refers to the elephant's friendships with other elephants of the same gender, hence, this non-significant association could mean that allomothers tend to bond more frequently with other female members of the group than non-allomothers (which is a part of establishing allomothering bonds with another female's offspring).

Further inquiries into allomothering behavior in elephants would benefit from using larger sample sizes, which would increase the statistical power. A statistical power analysis should provide insight into an appropriate sample size for the intended analysis. However, collecting data on elephants can be especially challenging due to their large geographical range, potential danger to humans, legal protection, low reproduction rate, and high cost. Therefore, future efforts should explore alternative statistical methods to investigate the potential link between allomothering and personality factors using small sample sizes. In this study the small sample size limited research to the use of observed instead of latent variables for the study of the link between personality and allomothering. Using latent variables is preferred because it can reduce measurement error by accounting for the shared variance among observed variables and extracting the common factor that they are intended to measure. This can improve the reliability of statistical analyses and facilitate more accurate conclusions regarding personality.

Another potential limitation is the use of subjective personality assessments. Although behavioral assessments were done by trained animal keepers, subjective assessments can still be a potential source of bias and error. For instance, the context of the study, such as the presence of other animals, environment, and time of day, can impact the interpretation of results and influence the way behavior is perceived and recorded. There is a multitude of evidence supporting the validity, consistency, and reliability of subjective assessments of behavior as long as they are performed by experienced observers (e.g., Barnard et al., 2016; Carter et al., 2012; Ijichi et al., 2013; Tetley & O'Hara, 2012; Uher & Asendorpf, 2008). Still, it should be highlighted that the industry is experiencing high rate of job turnover, meaning that oozies may be younger and less experienced (Crawley et al., 2019). Further research should be performed to assess how much experience is needed to obtain reliable observations of allomothering behavior. However, a recent study found that non-specialist oozies and more experienced oozies consistently and accurately identified stress-related behavior in elephants (Webb et al., 2020).

Future research should dive deeper into the factors that influence and maintain healthy allomothering relationships. By doing so, we can gain a valuable insight not only of the evolutionary pressures driving allomothering, but also of the factors that make certain temperaments flourish in specific contexts. This knowledge is vital for the progression of ecological and evolutionary theory, as well as for the practical implementation of conservation efforts for the growing number of captive and semi-captive animal populations.

5. Conclusion

I investigated allomothering behavior in a semi-captive population of Asian elephants working in Myanmar's timber industry over a four-year period. I confirmed the repeatability of allomothering in this population but found no significant association between allomothering and personality-related behaviors using a small sample size. I suggest that further investigation with a larger sample size is needed to accurately evaluate the link between personality and allomothering. I also found that captive-born elephants are more likely to exhibit allomothering behavior than wild-caught elephants. Future research should aim to delve deeper into the underlying mechanisms that help maintain healthy allomothering relationships.

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Supplementary material

Supplementary material 1. Data exploration

Table 1. Additional summary statistics of sample data

	Study sample for the analysis of the repeatability of allomothering behavior	***Study sample for the analysis of the link between allomothering and personality***
Total amount of workgroups and calves available in workgroups	34 workgroups ● 20 workgroups had 1 calf (~59%) ● 4 workgroups had 2 calves (~12%) ● 5 workgroups had 3 calves (~15%) ● 3 workgroups had 4 calves (~ 9%) ● 1 workgroup had 5 calves (~3%) ● 1 workgroup had 6 calves (~3%)	20 workgroups: ● 15 workgroups had 1 calf (75%) ● 3 workgroups had 3 calves (15%) ● 2 workgroups had 4 calves (10%)

Visual data exploration

Ratings refer to all the observations reported for an elephant throughout the four-year study. *Individuals* refers to study subjects, and I show the most recent observations for each study subject.

I. Visual data exploration of repeatability sample

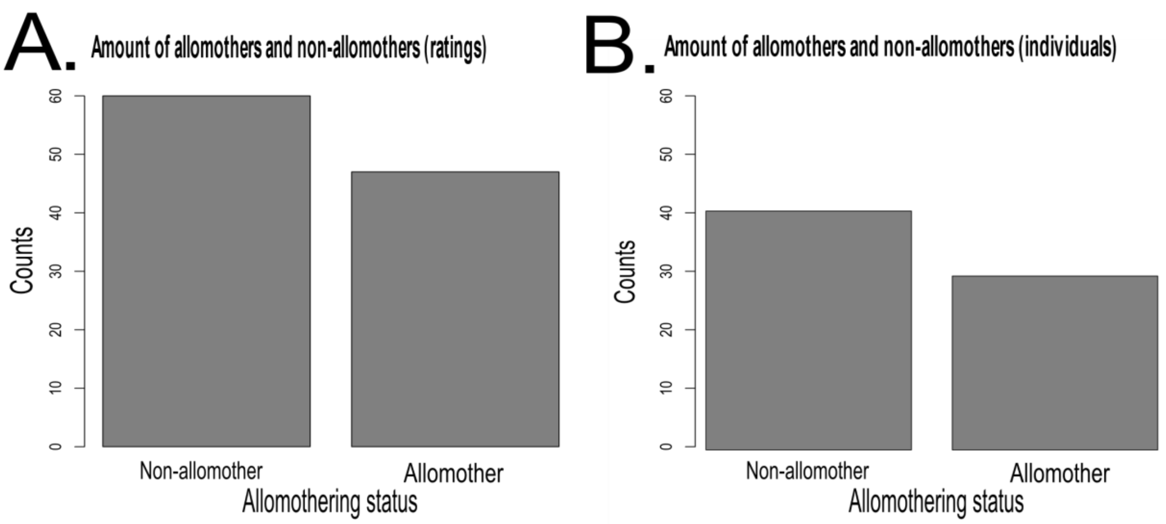


Figure 1. Number of allomothers and non-allomothers observed in the repeatability sample. (a) allomothering status (ratings); (b) allomothering status (individuals).

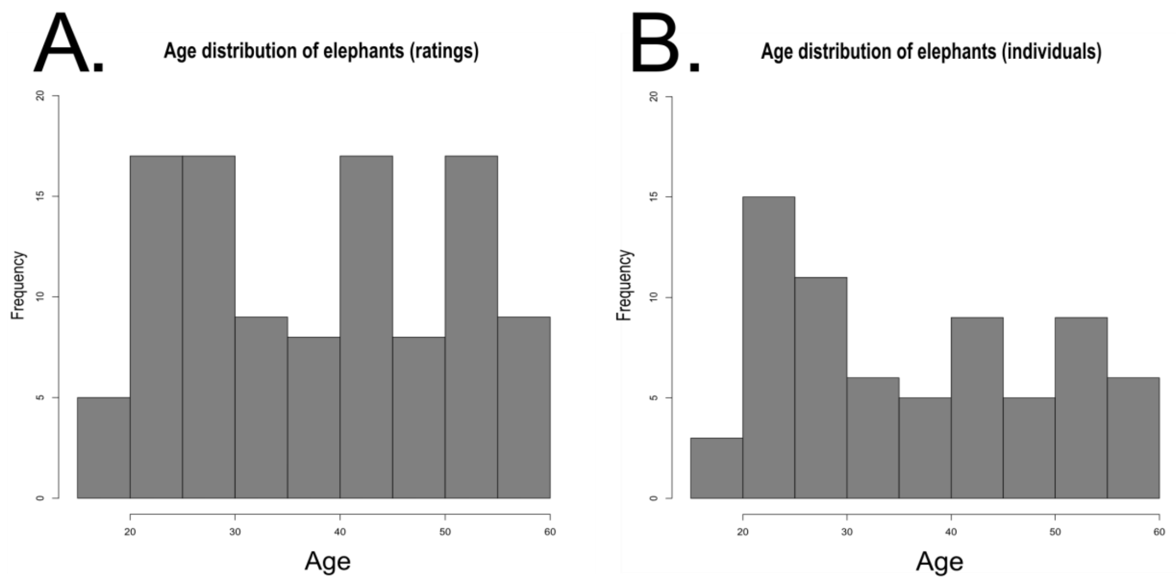


Figure 2. Age distribution of elephants in the repeatability sample. (a) age distribution of elephants (ratings); (b) age distribution (individuals).

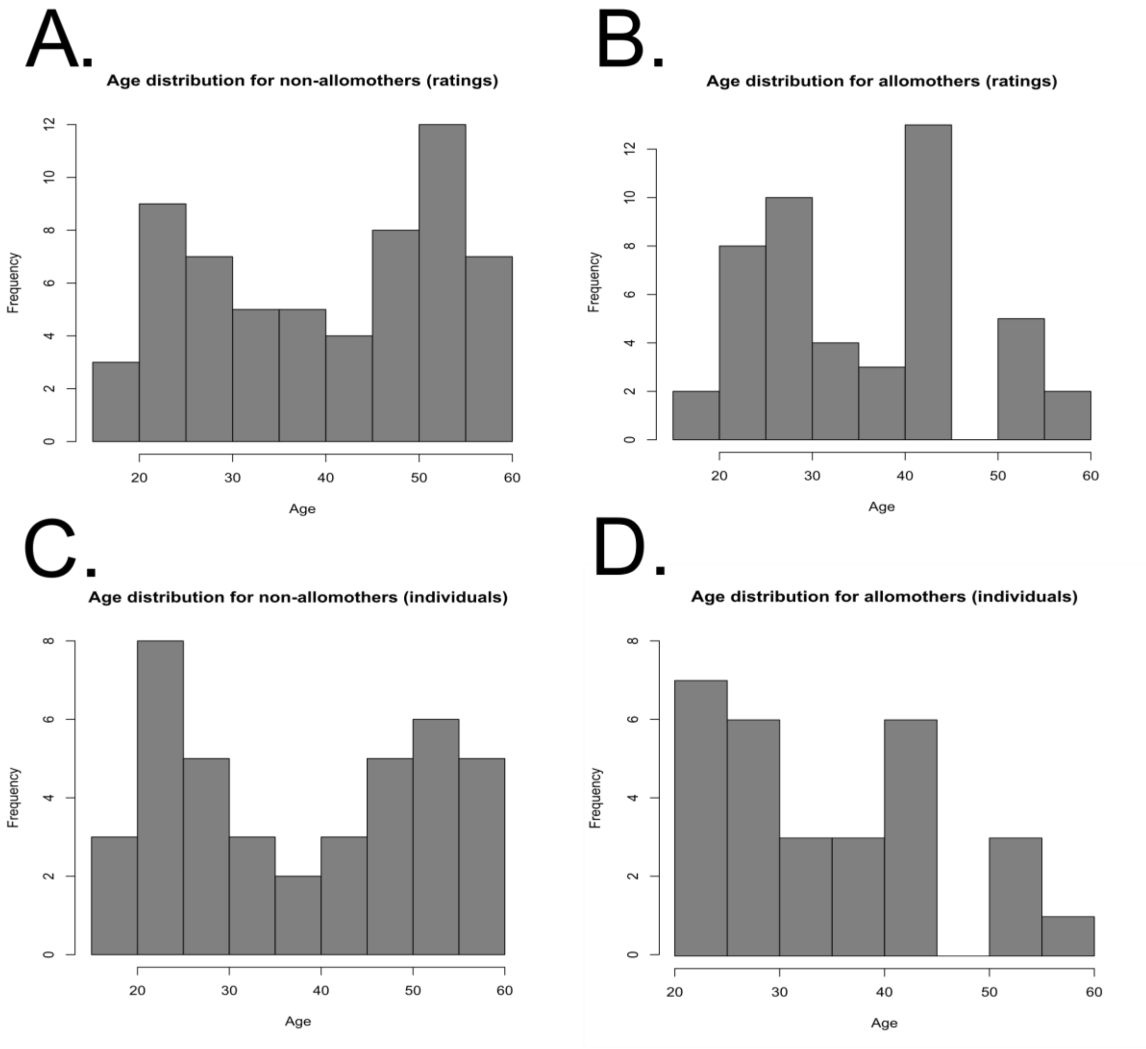


Figure 3. Age distribution of allomothers and non-allomothers in the repeatability sample. (a) age distribution of non-allomothers (ratings); (b) age distribution of allomothers (ratings); (c) age distribution for non-allomothers (individuals); (d) age distribution for allomothers (individuals).

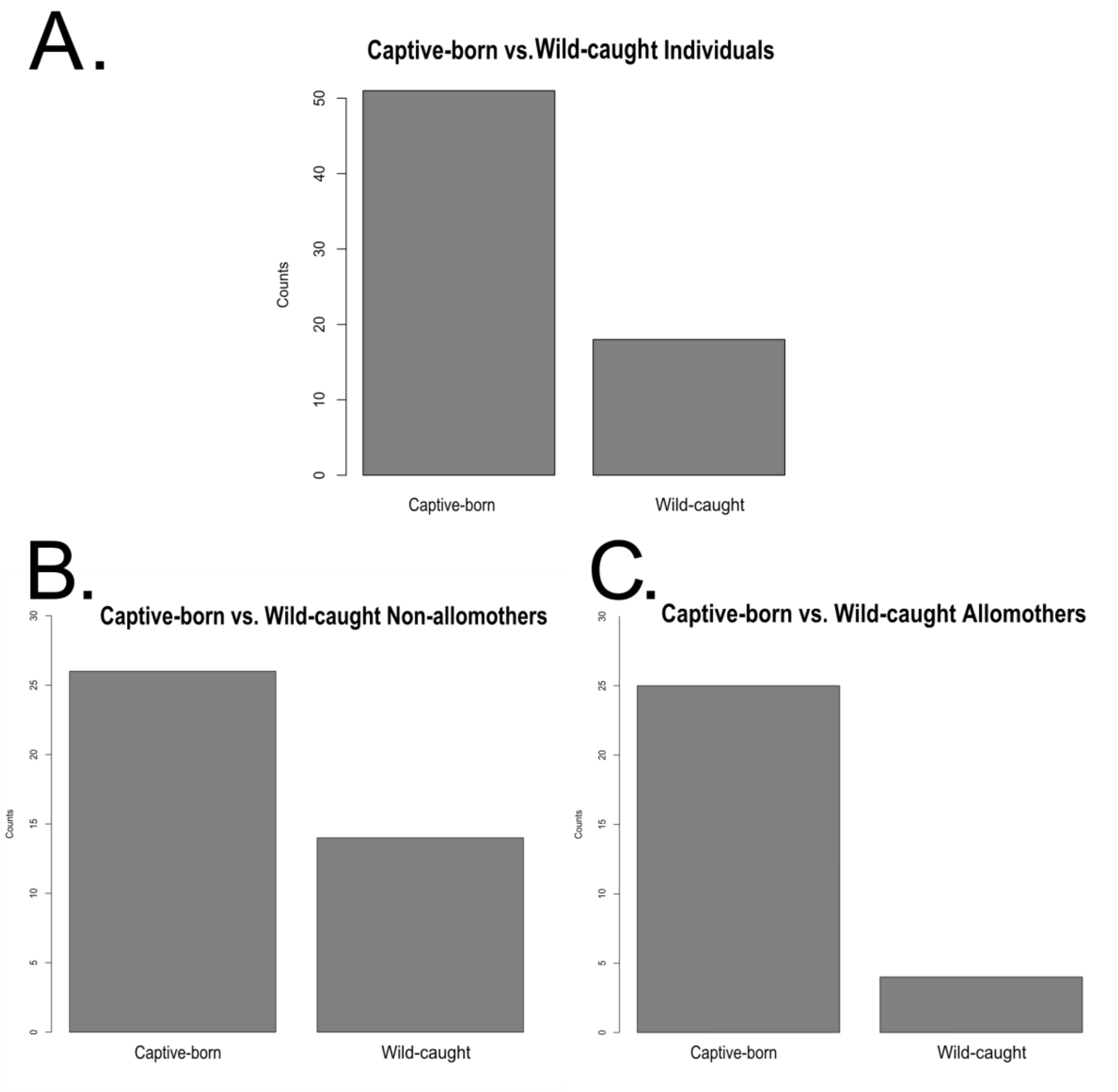


Figure 4. Origin of elephants in the repeatability sample. (a) origin of all elephants in the sample (individuals); (b) origin of non-allomothers (individuals); (c) origin of allomothers (individuals).

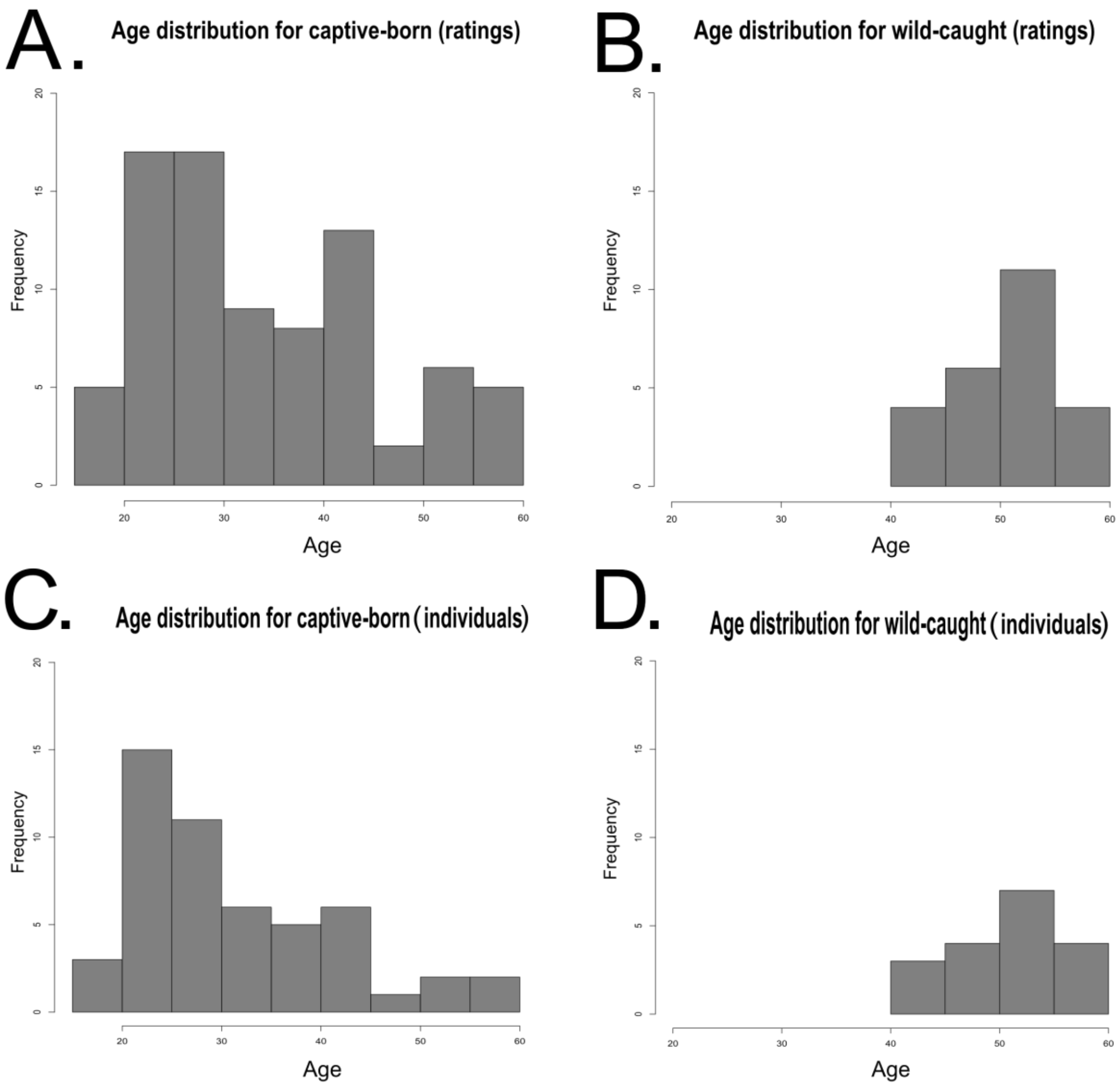


Figure 5. Age distribution according to origin of elephants in the repeatability sample. (a) age distribution of captive-born elephants (ratings); (b) age distribution of wild-caught elephants (ratings); (c) age distribution of captive-born elephants (individuals); (d) age distribution of wild-caught elephants (individuals).

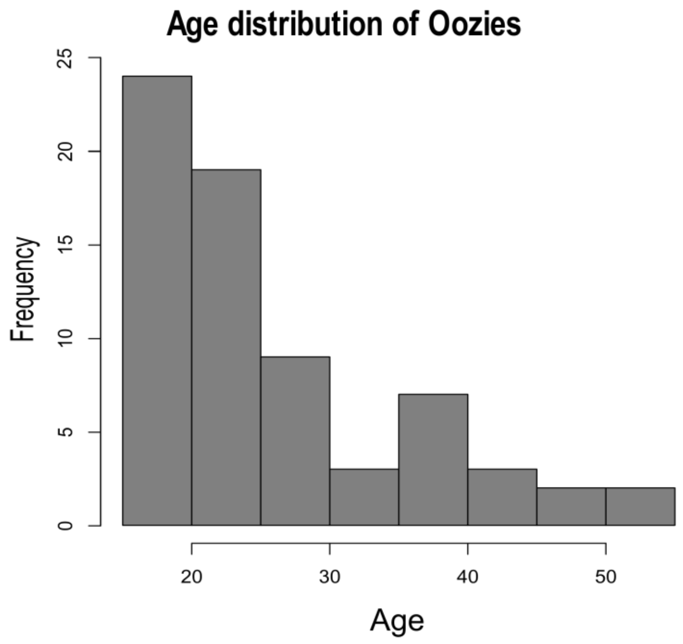


Figure 6. Age distribution of oozies in the repeatability sample. Showing the most recent age reported.

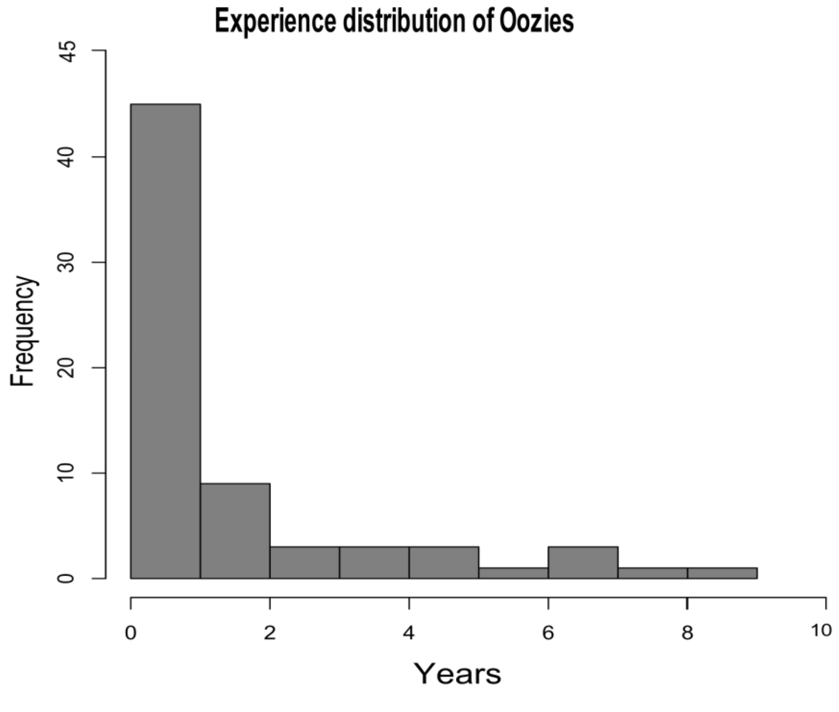


Figure 7. Experience distribution in years reported by oozies in the repeatability sample. Showing the most recent amount of experience reported.

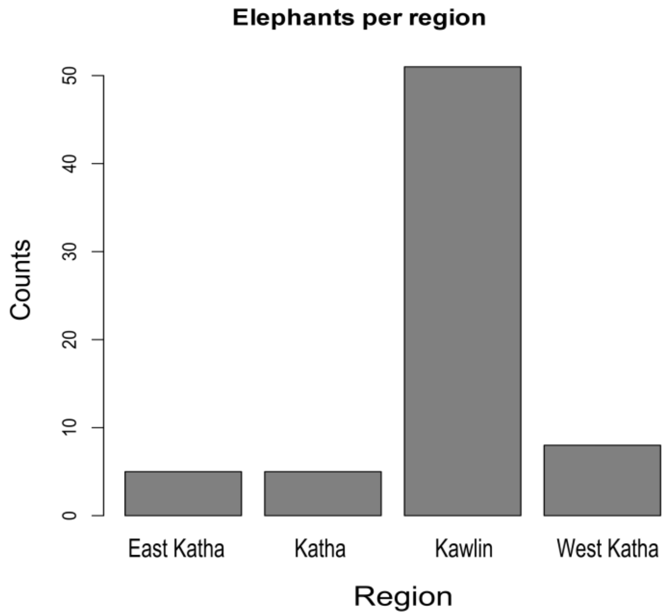


Figure 8. Elephant camp regions represented in the repeatability sample.

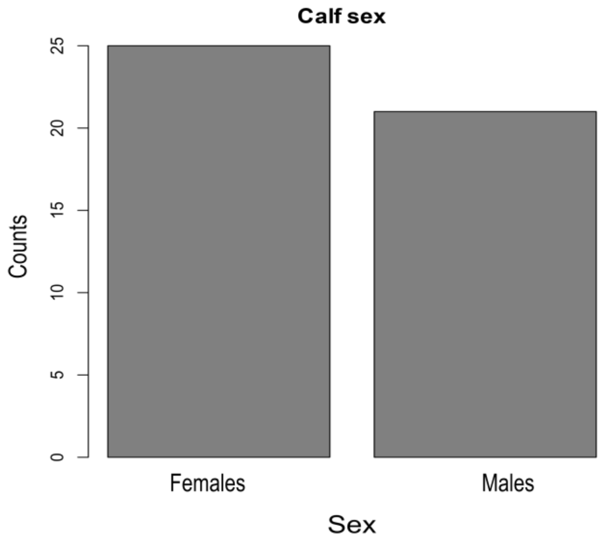


Figure 9. Calf sexes reported in the repeatability sample. Showing the calf sex reported across all ratings.

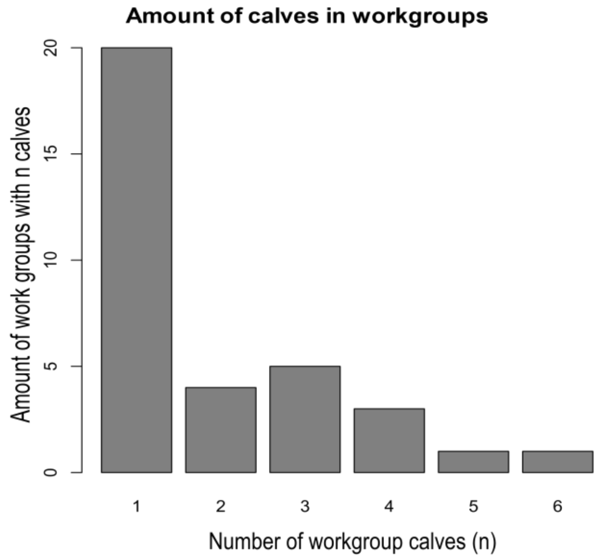


Figure 10. Amount of workgroup calves per workgroup in the repeatability sample.

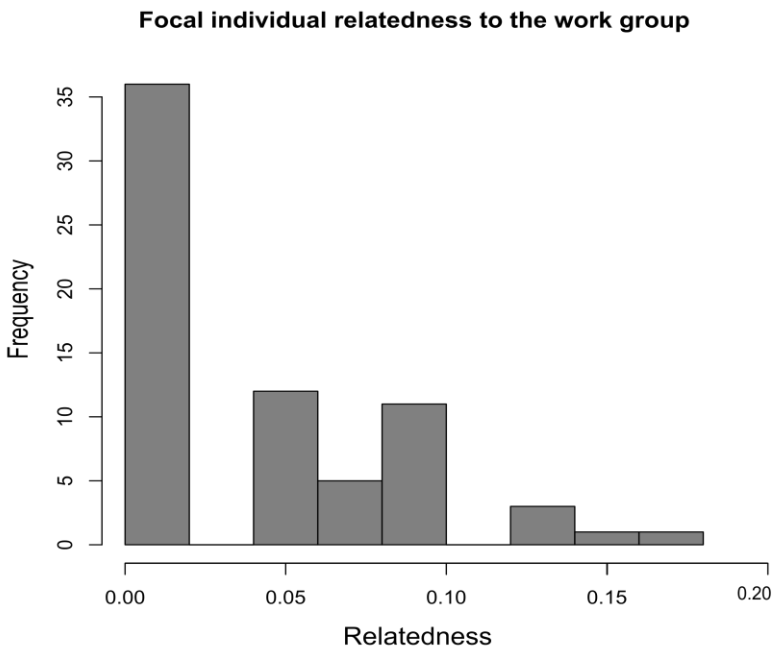


Figure 11. Relatedness of focal individuals to their respective workgroup in the repeatability sample. The relatedness of the focal elephant to the rest of the workgroup is the average relatedness to the other members of the workgroup.

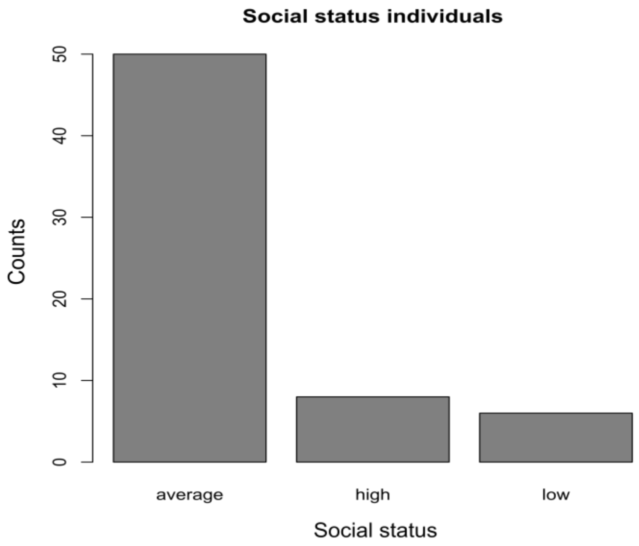
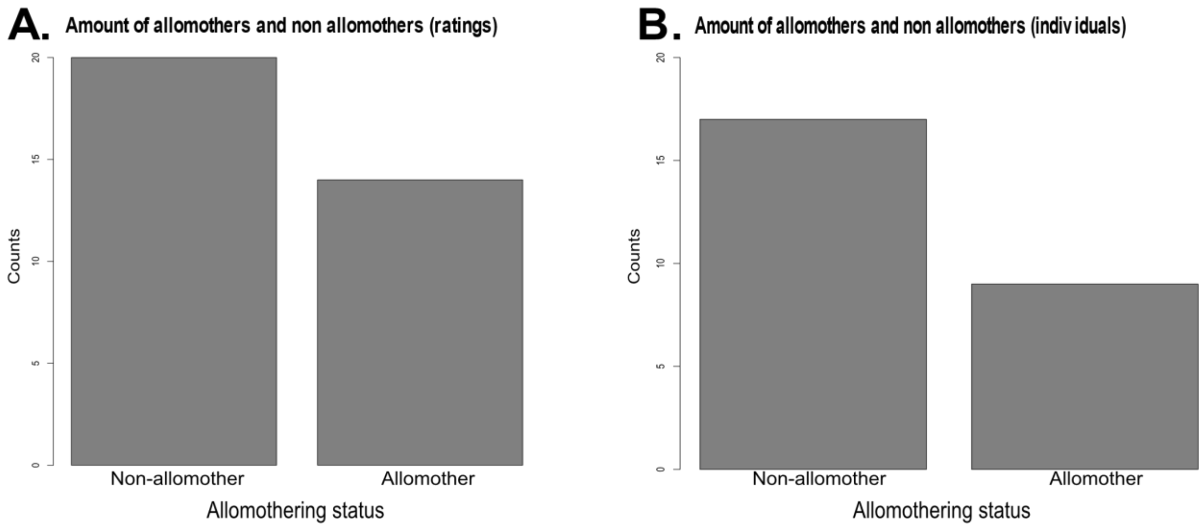


Figure 12. The social status of elephants reported in the repeatability sample.

II. Visual data exploration of the personality sample



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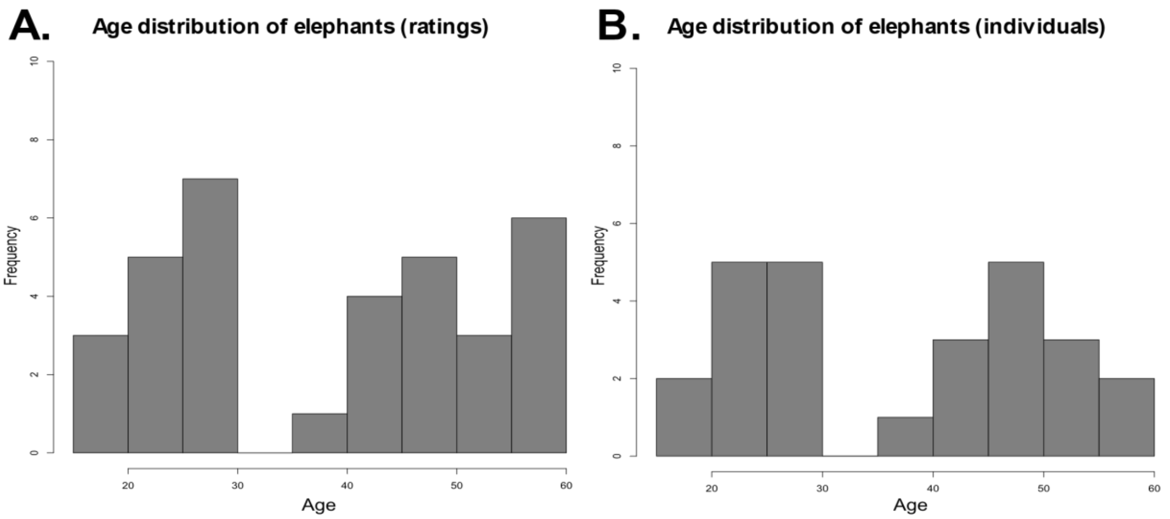

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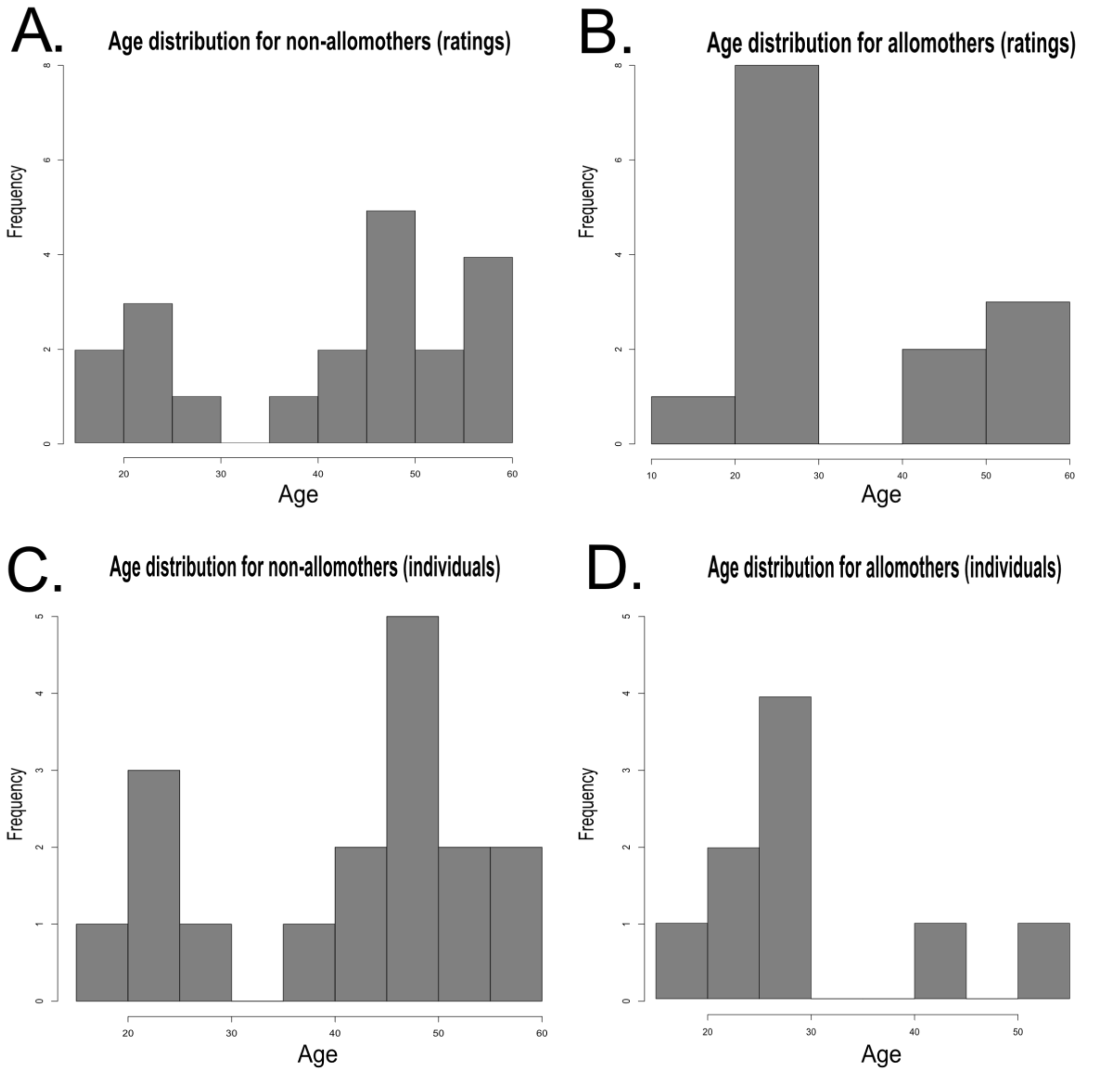

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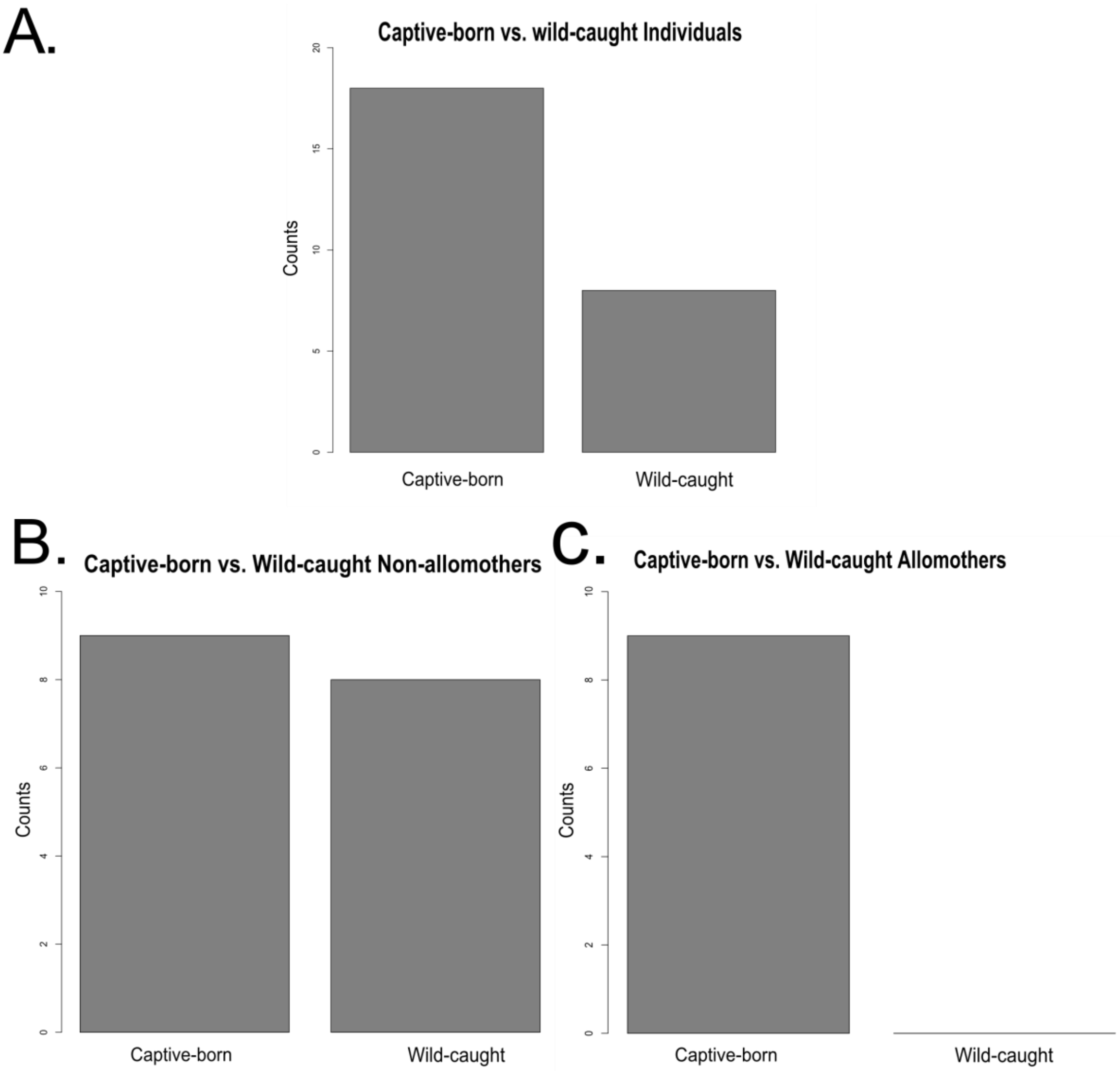

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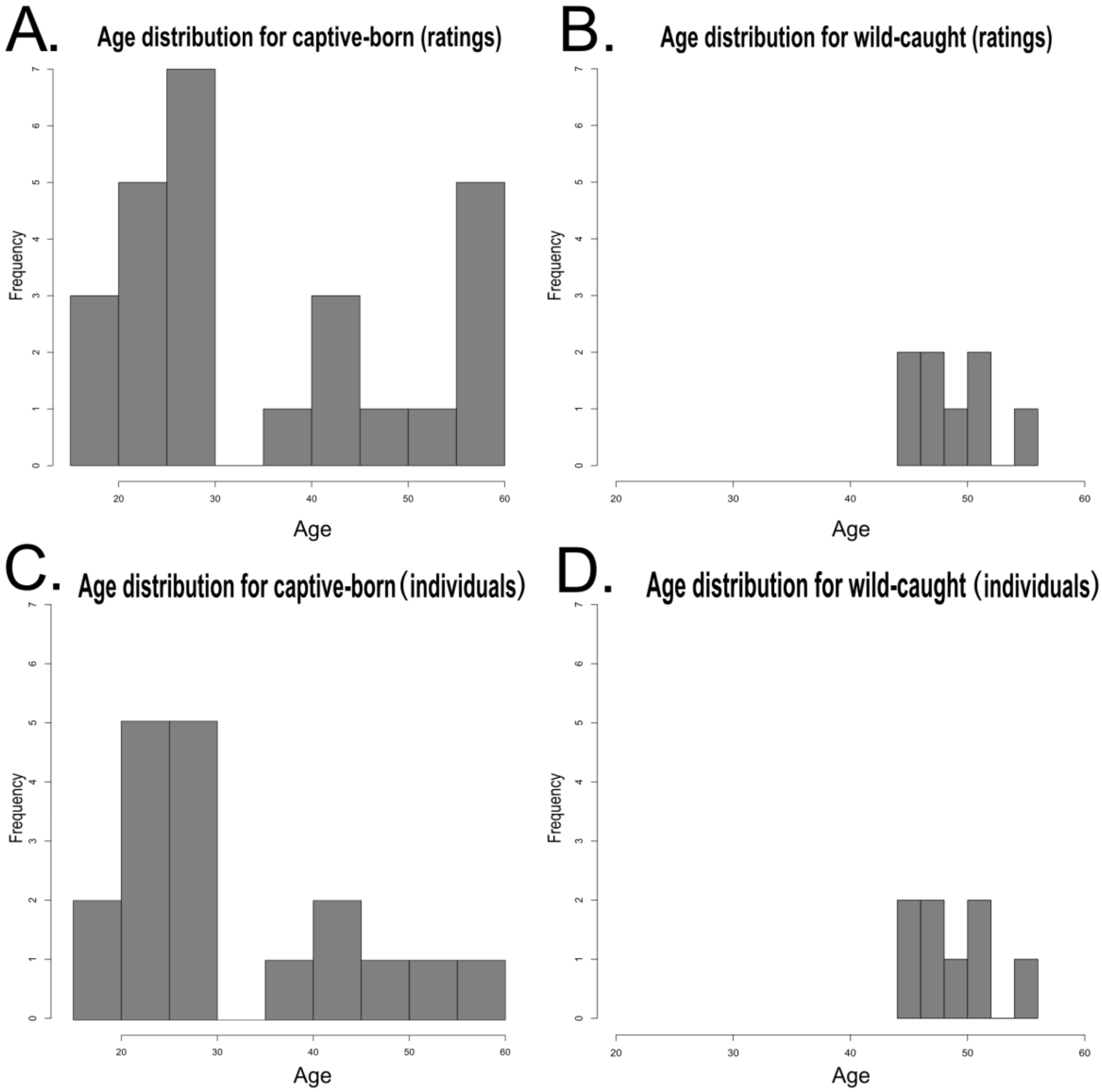

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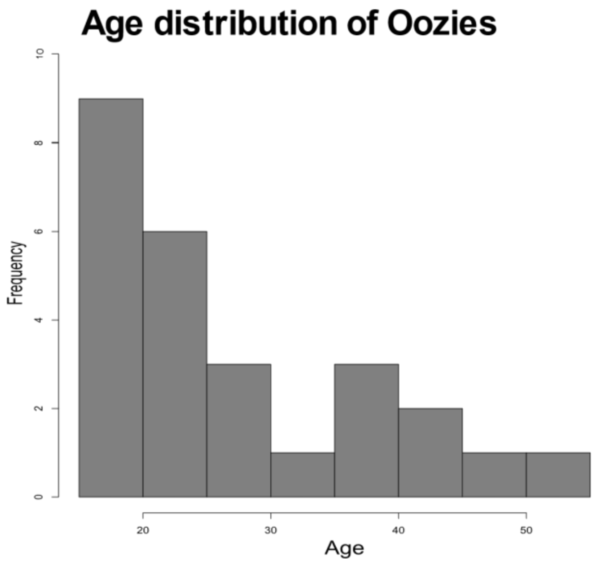
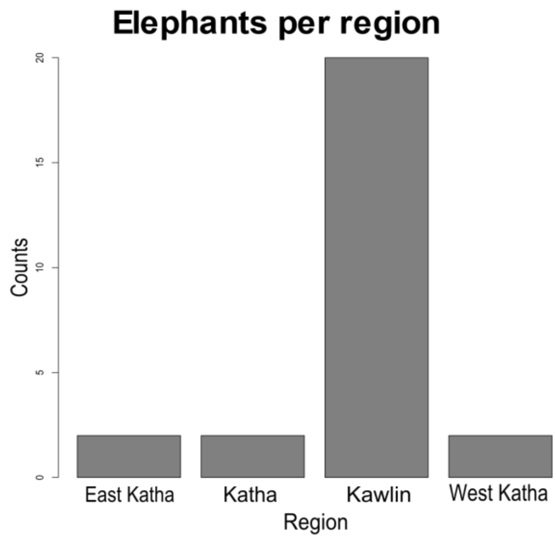


6. Age distribution of oozies in the personality sample. Showing the most recent age reported.

Figure 7. Experience distribution in years reported by oozies in the personality sample. Showing the most recent amount of experience reported.



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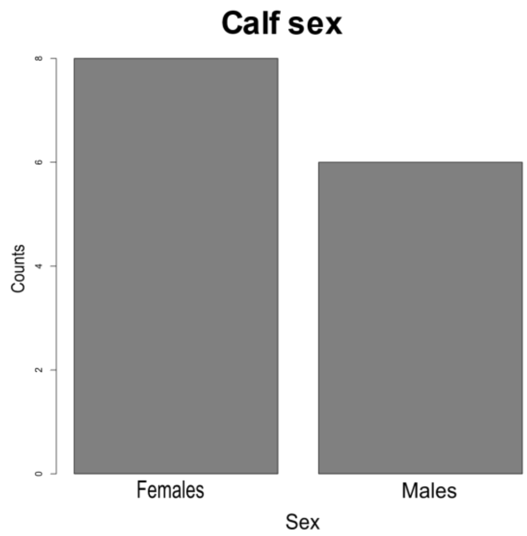

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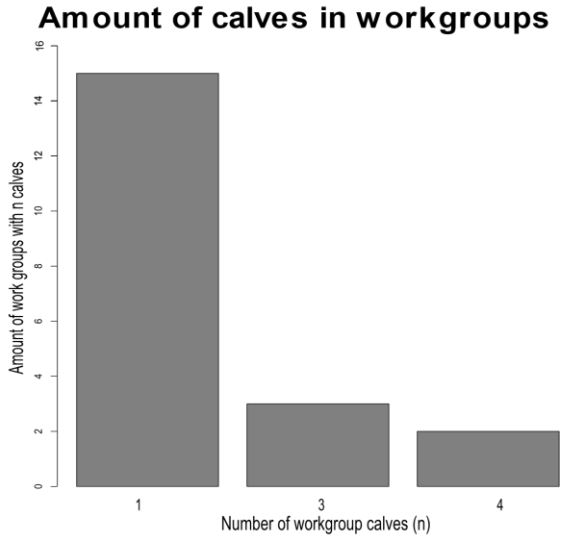

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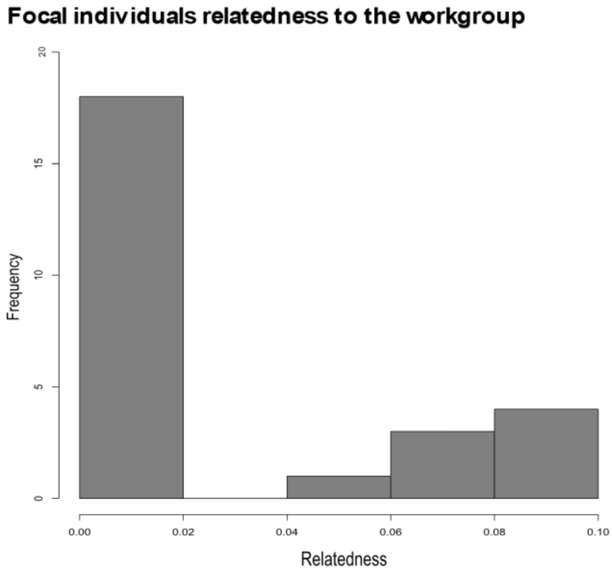

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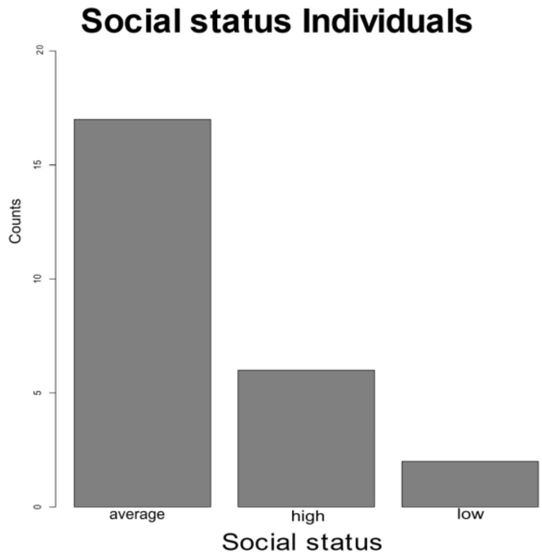

Figure 12. The social status of elephants that was reported in the personality sample.

Supplementary material 2. Social questionnaire.

Social relationships (part 1) and auntie/allomother (part 2) questionnaire for adult elephants

To be presented for the oozie (main head rider) of adult MALES and FEMALES.

Note: Part 1 for ALL adult elephants, Part 2 for females who have currently calves-at-heel or have given birth during the past 5-6 years.

Elephant Name and Sex (M/F):____

MTE number: ____

Elephant camp and state/region: ____

Oozie's name:____

Oozie's Age: ____

When the oozie started working with the elephant?: year ________ month________

Date of the questionnaire (dd/mm/yy):_____________

Indicate the given rating by marking the box with a cross underneath the chosen rank [X]

PART 1

FOR ALL MALES AND FEMALES

SOCIAL ORGANISATION

1. **MTE working group**
   Please list the **MTE number** (or **name and age** if number not known) of the other group members

2. Free time group

2.1 SOCIAL STATUS. How dominant the elephant is in relation to others in familiar environment **ie. own group during free time among same sex individuals**?

High Status	Average	Low-status	I don't know

2.2 BEST ADULT FRIENDS during free time. List the MTE number (or **name and age** if not known) of the **adult** elephant(s) closest to this elephant.

if usually **alone** and has no close friends tick the box below

2.3 What does the friend usually do with the elephant? Please write in the box the MTE number (or name) of the friend(s) showing the behavior. You can put several friend numbers in the same box.

Play	Fight	Take care of the calves	Eat	Vocalize	Touching, grooming	Work	Else, what?

PART 2

Fill this part of the questionnaire for those adult females who currently have a calf-at-heel, or have given birth to a calf during past 5-6 years AND if the same

oozie was the main head rider then. Comments can also be added to clarify the oozie's answer or give extra information on allomothering.

PREVIOUS CALF/CALVES

1. **Current calf-at-heel name and age OR previous** calf (born during past 5-6 years) **MTE number** (or **name and age** if unknown):

____

2. **How long was the calf allowed to stay full-time with the mother**? If the calf is still full-time with mother, tick the box, 'still fulltime'.

1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	5+ yrs.	still fulltime	I don't know
☐	☐	☐	☐	☐	☐	☐	☐

3. **Calves that have already started training:** does the calf continue having opportunity to spend time with mother **e.g. during nights, free time or rest periods**?

Very often	Sometim e	Rarely	Never
☐	☐	☐	☐

4. **What age was the calf weaned from the mother?** If still lactated by the mother, tick the box 'still lactated'.

1 yr.	2 yrs.	3 yrs.	4 yrs.	5 yrs.	still lactated	I don't know
☐	☐	☐	☐	☐	☐	☐

5. **Have you or other MTE staff ever given some extra-food of nutritional value to the calf? Including also treats like tamburins.**

yes no I don't know

5.1 If **yes**, how often?

Very often (daily)	Often	Sometimes	Rarely

6. Do/Did other females ("aunties/allomothers")(including juvenile siblings and unrelated females) take care of the calf during free time or work time?
(if "no" or "I don't know", skip the rest of the questions)

yes	no	I don't know	Other females would like to but the mother does not allow

6.1 If **yes,** which (adult or juvenile **females**)? **Please** give the MTE number **or name and age** if unknown.

7. Did you see these females ever lactating the calf (allo-lactation)?

yes	no	I don't know

7.1 If **yes**, which females? Please give the MTE number **or name and age** if unknown.

8. **What does the "auntie/allomother" (adult or juvenile female or sibling) usually do with the calf?** Please write in the box the **MTE number (or name)** of the auntie(s) showing the behavior. You can put several auntie numbers in the same box, if the same auntie both often lactated and played with the calf.

lactate the calf	play with the calf	protect the calf	help with food items	rest with the calf	travel with the calf	else, what?

9. How often is/was each auntie (allomother) seen with the calf (tick relevant box for each auntie) during **free resting time or work time**? For example, during the past year how often the calf has been found from the forest in the morning close-by to this auntie.

Auntie **MTE No or name**:	Nearly always	Often	Some-times

10. **Has the same auntie been an auntie to this mother's previous calves too?**

yes	no	I don't know

10.1 If **yes,** which auntie (name or MTE number)

____