

Increasing browse and social complexity can improve zoo elephant welfare

Running Title: Factors Influencing Zoo Elephant Behavior

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Abstract

While recent work has assessed how environmental and managerial changes influence elephant welfare across multiple zoos, few studies have addressed the effects of management changes within a single institution. In this paper, we examine how management changes related to social structure and diet affect the behavior of a group of zoo elephants over a 23-month period while also considering underlying factors such as time of day, hormonal cycle, and individual differences. We recorded individual behaviors recorded using two-minute scan samples during 60-minute sessions. We analyzed behavioral changes across several study variables using generalized linear mixed models. We found that increasing browse can improve opportunities for foraging throughout the day but may not be sufficient to reduce repetitive behaviors. We observed that increasing group size and integration of bulls with cows can lead to increased social interaction in African elephants. Our results highlight the importance of using multiple management alterations to address elephant welfare, and considering environmental factors, when making management decisions.

Keywords: behavior, *Loxodonta africana*, management, *ex situ*

1 **1. Introduction**

2

3 African elephants (*Loxodonta africana*) are a highly social and cognitively-complex species (e.g.,
4 quality judgment, elaborate communication schemes, etc.; Grand et al., 2012) that have intricate needs.
5 Captive facilities should consider these needs in the effort to optimize the welfare of elephants in human
6 care. Recent comparative studies provide insights into how housing, diet, social structure and other
7 factors relate to elephant welfare status (Azevedo et al., 2016; Barber, 2018; Bjork, 2011; Garaï, 1992;
8 Greco et al., 2016; Horback et al., 2014; Koyama et al., 2012; Kurt and Garaï, 2001; Lehnhardt, 2006;
9 Mason and Veasey, 2010; Meehan et al., 2016; Menargues et al., 2008; Posta, 2011; Price and Stoinski,
10 2007; Rees, 2009; Schmid et al., 2001; Vanitha et al., 2011; Veasey, 2006; Wiedenmayer, 1998), but do
11 not directly assess how management changes within an elephant herd affect behavior. Longitudinal
12 studies that consider both management factors and external factors are needed to inform elephant care and
13 better understand elephant behavior.

14 Changes in diet have had positive impacts on welfare across several zoo-housed species
15 (Azevedo et al., 2016; Barber, 2018; Bjork, 2011; Greco et al., 2016; Horback et al., 2014; Koyama et al.,
16 2012; Posta, 2011; Rees, 2009; Wiedenmayer, 1998). Browse (i.e., woody material such as tree branches)
17 availability is important for gut health and combating obesity due to increases in fiber content (Bjork,
18 2011; Greco et al., 2016; Harris et al., 2008; Meehan et al., 2016; Morimura and Ueno, 1999; Stoinski et
19 al., 2000; Veasey, 2006; Wiedenmayer, 1998). Increasing woody browse items is associated with
20 increased time needed for food processing and is positively correlated with feeding behaviors and general
21 activity in African elephants (Stoinski et al., 2000).

22 Alterations in social group complexity and size can improve the welfare of zoo-housed animals
23 (Garaï, 1992; Kurt and Garaï, 2001; Lehnhardt, 2006; Mason and Veasey, 2010; Meehan et al., 2016a,b;
24 Menargues et al., 2008; Posta, 2011; Price and Stoinski, 2007; Schmid et al., 2001; Vanitha et al., 2011;
25 Veasey, 2006). Negative welfare indicators (e.g., high levels of aggression, lethargy, health issues, or
26 stereotypic movement) decreased with increasing group size (Rees, 2009; Vanitha et al., 2011) and

27 complexity of social groupings (such as larger groups with differences between individuals in terms of
28 age, sex, etc.) across multiple zoos (Greco et al., 2016). Increasing 1) chances for social interaction by
29 increasing group size and 2) social group complexity by varying social groupings within a captive
30 elephant group may, therefore, improve welfare.

31 While management changes such as diet and social grouping can influence behavior, it can be
32 important to account for other underlying factors, such as time of day, hormone cycling, and individual
33 differences when considering zoo animal behavior. Zoo-housed animal behavior is often affected by daily
34 temporal variation. Rees (2009) found that repetitive behaviors displayed by zoo elephants increased in
35 frequency towards the end of the day, and others have suggested that repetitive behaviors in elephants are
36 anticipatory, specifically occurring in greater frequency directly before and after mealtimes (Mackey,
37 2014). Researchers have observed multiple differences between diurnal and nocturnal activity budgets,
38 such as increases in positive social behaviors during the day, an increase in self-maintenance behaviors
39 early morning and late evening (Horback et al., 2014), and repetitive behaviors with the lowest
40 occurrence in the morning (Hasenjager and Bergl, 2015). It is thus important to be aware of time of day
41 effects on behavior in observational studies of zoo-housed animals.

42 Hormone levels and cycling can also affect behavior. Elephants experience patterned hormone
43 cycles, and these changes can be associated with specific behaviors (or behavioral profiles). Wild female
44 elephants increase socially-motivated interactions with other females during ovulation (Freeman et al.,
45 2010), and males engage in more positive interactions with cows and negative interactions with bulls
46 during musth (Ganswindt et al., 2005; Hollister-Smith et al., 2007; Ortolani et al., 2005; Thitaram et al.,
47 2009).

48 In cognitively complex species, individual differences (e.g., personality, life history traits, and
49 previous experience) are frequently highlighted during welfare assessments (Grand et al., 2012; Horback
50 et al., 2013; Lee and Moss, 2012; Yasui et al., 2013). Horback et al. (2013) explained how the ability of
51 zoos to discern elephant personalities reliably can allow caretakers to identify appropriate roles (e.g.,
52 social compatibility) and welfare needs for individual animals (e.g., appropriate environmental

53 enrichment or optimal training methods). Individual differences make generalized conclusions on group
54 behavior difficult, so behavioral observations are arguably best conducted on an individual, rather than
55 group, level (Grand et al., 2012; Lee and Moss, 2012; Yasui et al., 2013).

56 It is challenging to determine how husbandry management changes might affect welfare since
57 many factors can influence elephant behavior (Holdgate et al., 2016; Horback et al., 2014; Koyama et al.,
58 2012; Meehan et al., 2016a,b; Posta, 2011; Posta et al., 2013; Rees, 2009a,b; Wilson et al., 2004). While
59 recent work has assessed variation across institutions and how managerial and environmental factors
60 influence elephant welfare, few studies have assessed the effects of multiple environmental and
61 managerial changes over an extended period of time within one group. In this paper, we analyze how
62 changes in social structure and diet affected the behavior of a group of elephants housed at the North
63 Carolina Zoo (NC Zoo) over a 23-month period, while also considering non-management factors such as
64 time of day, hormone cycling, and individual variation. We predicted that the diet alteration would
65 increase the frequency of foraging and locomotion and decrease the frequency of repetitive behavior. We
66 also predicted that an increase in group size and composition complexity would lead to an increase in
67 social and locomotive behaviors, as well as a decrease in repetitive behaviors. We hypothesized an
68 increase in social behavior observed between elephants during phases with high hormonal output (i.e.,
69 musth for male elephants and luteal phase for female elephants). We also predicted that foraging and
70 repetitive behavior would show temporal variation. By considering how management and environmental
71 variables can alter behavior, we are able to provide insights into how we can adapt husbandry changes to
72 improve captive elephant welfare.

73

74 **2. Materials and Methods**

75

76 *2.1. Behavioral Observations*

77 The NC Zoo (Asheboro, NC, USA) houses six African elephants on two three-acre exhibits
78 during the day when temperatures are above 40 °F. The elephant herd consists of two male elephants

79 (ages 34 and 43 years old) and four female elephants (ages 15, 29, 35, and 39 years old). While two
80 females are a cow-calf pair, no other individuals housed at the facility are related. Observers collected
81 behavioral data on elephants between the hours of 0900 and 1700 from January 2015 to November 2016;
82 observers collected scan samples every two minutes in hourly scans randomly throughout the day.
83 Observers watched elephants from visitor viewing platforms that provided nearly unobstructed views of
84 the elephants' enclosure spaces. Observers used an ethogram created by Hasenjager and Bergl (2015) to
85 record elephant behavior (Appendix 1). At the beginning of each session, observers recorded the number
86 and names of the elephants present within the exhibit. We recorded observations in real-time in
87 ZooMonitor (Ross et al., 2016). Initially, observers recorded behavior of a single individual, but
88 beginning in January 2016, observers recorded behavior of all elephants present in the exhibit during each
89 scan, which greatly increased data collection and was feasible since there were never more than five
90 elephants in a given exhibit.

91

92 *2.2. Husbandry Alterations*

93 Keeper Schedule: Though keeper schedule can be variable, keepers would arrive at the elephant
94 facility in the morning and supply elephants with hay and conduct training sessions in the barn. Keepers
95 would also clean outdoor habitats at this time. Keepers released elephants onto habitat later in the
96 morning (09:30-10:30), and interacted with the elephants for public display around 13:30-14:30 every
97 afternoon. Keepers returned elephants to the barn for the evening around 15:00-16:00, although elephants
98 were given access overnight where possible. Keepers altered elephant social groupings as necessary
99 during habitat transfers and provided browse in the afternoon when possible (depending on availability).
100 We examined two changes in these husbandry practices for the African elephants at the NC Zoo: a change
101 in diet and a change in herd management and structure.

102 Changes in diet: In February 2016, zoo staff transitioned the elephants from a "high inclusion"
103 pellet feed (Wild Herbivore Plus at 10% of total dry matter diet) to a "low inclusion" diet with a grain-
104 free pellet feed (Mazuri Hay Enhancer at 5% of dry matter diet) (Wood et al., in press). Concomitantly,

105 the zoo increased the amount of browse provided from one truckload per week to one truckload daily and
106 increased the distribution of hay from 2 bales prior to February 2016 to 2.5 to 3 bales of hay afterward.
107 This allowed us to assess behavioral changes pre (January 2015 to January 2016) versus post (February
108 2016 to November 2016) diet change.

109 Changes in herd structure management: At the beginning of the study, the zoo managed four
110 cows in two separate pairs and two bulls separately as individuals. In March 2015, the zoo began
111 introducing Male 1 to Females B and C, so that all three elephants shared the same space. On March 26,
112 2015, Male 2 was introduced to Females A and D. In July 2015, the two female pairs were introduced.
113 After successful introductions, elephants could be housed in larger groups, and staff used a variety of
114 different herd structures to increase social complexity. We collected data on elephant behavior across the
115 different group sizes, ranging from 1 to 5 for males and 2 to 5 for females, and for the females with and
116 without the presence of a male.

117

118 *2.3. Hormone Data Collection*

119 We extracted each subjects' hormone cycle history from the Species360 ZIMS (Zoological
120 Information Management Software) online database. Keepers determined male musth cycles using the
121 following well-documented indicators of hormonal fluctuations in the species (Duer et al., 2016):
122 temporal gland drainage, head pressing (pressing forehead onto bars of enclosure, possibly to relieve
123 cranial pressure), quicker movement, continuous urination, and increased distractibility during training
124 sessions. Musth indicators are visual and each staff member is trained to recognize musth in bull
125 elephants in accordance with safety protocols. Keepers communicate with each other prior to noting
126 behavioral musth indicators in the daily log so these behaviors can be verified by all keepers working for
127 the day. Staff members did not record the intensity or hormonal status of musth, only the presence of
128 musth-related behaviors.

129 We determined female estrus cycling patterns via serum estrogen levels from blood samples
130 taken every two weeks. Blood is collected from a vein on the back of the ear using a 21- or 19-gauge

131 needle on a weekly schedule as part of normal husbandry management and serum is sent to the
132 Smithsonian Endocrine Lab for hormone analysis (Graham et al., 2001). Samples are measured for each
133 individual's progesterone levels with an enzyme immunoassay. The enzyme immunoassay is a double
134 antibody immunoassay using primary antibody anti-progesterone CL425, and secondary antibody goat
135 anti-mouse IgG immobilized to a microplate. Staff members recorded these immunoassay results in
136 Species360 ZIMS. Hormone status was categorized as musth or non-musth for males and as follicular or
137 luteal phase for females.

138

139 *2.4. Time of day*

140 We categorized times of day into morning (09:00 – 11:00), midday (11:00 – 13:00), and
141 afternoon (13:00-17:00). Because keepers sometimes shifted elephants off exhibit at 16:00, we included
142 four hours in the afternoon period and two hours in the morning/midday categories to even out sample
143 size across categories.

144

145 *2.5. Statistical Analysis*

146 We broke down elephant behavior data into frequencies for a given scan (i.e. number of
147 observations displaying a given behavior out of 30 two-minute scans recorded) with a focus on five key
148 behaviors: resting (standing, lying down), foraging (on prepared diet, exhibit vegetation, or browse),
149 repetitive (rocking, pacing or other repetitive behavior; repetitive behavioral patterns such as pacing
150 patterns were previously conveyed to observers before conducting observations so they could recognize
151 such patterns), locomotion (walking or running non-repetitively), and social (vocalization, displacement,
152 agonistic or affiliative interactions between individuals). We did not distinguish between standing rest and
153 standing still without rest during our scan observations, as this would be very difficult to distinguish for
154 multiple observers.

155 Visibility of elephants was not a major issue during observations, but when an individual was not
156 visible, these observations were excluded from the total number of scans. We used the number of two-

157 minute scans in which an elephant was visible as a denominator for calculating relative frequencies of
158 each behavior. For animals in the same group measured simultaneously, we model the dependency of one
159 animal on others only through fixed effects for group size and whether or not a male was present in the
160 group. Ideally, a model would include a correlation structure that allowed us to estimate dependencies
161 between two individuals, but the sparseness of the data would not permit the fitting of such a model.

162 We attempted to obtain an even distribution of observations per individual and treatment,
163 however, all analyses were conducted in such a way to take uneven sample numbers into account. We
164 assessed the effects of (1) time of day (morning, midday, or afternoon) and diet change (before or after),
165 (2) hormone status (luteal or follicular for females and musth or non-musth for males), and (3) group
166 composition using three separate generalized linear mixed models based on the binomial distribution with
167 logit link function. These models included an overdispersion parameter and random subject effects to
168 account for repeated measurements on individual elephants. These models had fixed factorial effects for
169 group size and random effects for individual elephants, which do not require a balanced design for uneven
170 data sets. Pairwise comparisons and complex contrasts among levels of study variables or combinations
171 of study variables were carried out as appropriate when suggested by tests for interaction or for main
172 effects. Table 1 gives Akaike information criterion (AIC) and generalized chi-square statistics computed
173 from models with and without random observer effects, showing how the inclusion of random observer
174 effects is warranted. We also conducted pairwise comparisons between group sizes, and evaluated linear
175 interaction effects using a complex contrast of treatment means, and evaluated linear interaction effects
176 using a complex contrast of treatment means.

177 We made inferences using significance level 0.05. We fitted statistical models using PROC
178 GLIMMIX in SAS (2013). Graphs display error bars for standard error of each value.

179

180 **3. Results**

181

182 *3.1. Diet change effects on behavior, accounting for time of day*

183 We collected 397 hours of data over 96 days across the 23-month period. Observation budgets of
184 elephants in each social group, pre-diet change, and post-diet change can be found in Appendix II. Our
185 tests for factorial effects based on GLMMs provide evidence of an effect of time of day for every
186 behavior type. Resting ($F=122.77$, $p < 0.01$), social ($F = 9.25$, $p = 0.01$), and repetitive ($F = 88.56$, $p <$
187 0.01) behaviors increased over the course of the day while locomotion ($F = 4.39$, $p = 0.01$) and foraging
188 ($F=198.51$, $p < 0.01$) behaviors decreased throughout the day.

189 No behaviors were affected by diet change alone, but there was evidence of interactions of the
190 diet change on behavior by time of day. We found strong evidence that foraging behavior decreases over
191 time both before ($F = 94.60$, $p < 0.01$) and after ($F = 113.40$, $p < 0.01$) the diet change (Figure 1). The
192 decrease in foraging behavior from morning to the afternoon was significantly more pronounced before
193 the diet change than after ($t = 2.24$, $p = 0.03$). We found evidence of interaction between time of day and
194 diet change on frequency of social events ($F = 3.20$, $p = 0.04$). The frequency of social behavior increased
195 around midday (11:00 – 13:00) after the change in diet, whereas the increase did not occur until the
196 afternoon (13:00 – 17:00) before the diet change. F-ratios and p-values for tests for all factorial effects
197 involving time of day and diet change are given in Table 2.

198

199 *3.2. Effects of Hormone Cycle on Behavior*

200 Foraging ($F = 22.38$, $p < 0.01$), social ($F = 12.07$, $p = 0.0006$) and repetitive ($F = 4.08$, $p = 0.04$)
201 behavior frequencies of female elephants during luteal and follicular hormone cycles were significantly
202 different. Further, foraging ($F = 24.20$, $p < 0.01$), resting ($F = 26.96$, $p < 0.01$), social ($F = 4.36$, $p = 0.04$),
203 and repetitive ($F = 4.08$, $p = 0.04$) behavior differed when male elephants were in musth versus non-
204 musth. Repetitive and social behaviors were more frequent in female elephants in the follicular stage as
205 opposed to luteal stage while foraging behavior was less frequent. Males displayed decreases in foraging
206 and social behavior and an increase in repetitive behavior while in musth (Figure 2). Hormone cycle was
207 not a predictor for locomotion in either male or female elephants. F-ratios and associated degrees of
208 freedom and p-values for tests of these factorial effects are given in Table 3.

209 We further investigated the effect of hormone cycle on agonistic and affiliative behaviors
210 separately (Figure 3). Based on an F-test for equality of frequencies, affiliative behavior increased for
211 female elephants during the follicular stage ($t = 2.06$, $p = 0.04$). Note, when affiliative and agonistic
212 behaviors were considered separately (rather than both behaviors grouped into “social behavior” as a
213 whole), we did not observe differences in agonistic behavior for females or in either agonistic or
214 affiliative behavior for males across hormonal stage.

215

216 *3.3. Effects of Group Size and Complexity on Behavior*

217 Females displayed more social behavior (including both affiliative and agonistic behaviors) when
218 a male was present ($t = 2.49$, $p = 0.01$). Social behavior varied across group size ($F = 4.46$, $p = 0.002$),
219 and was greatest in a group size of 5 (Figure 4). Both affiliative and agonistic social behaviors were
220 positively association with group size (Figure 4). No other behaviors differed across group size at this
221 level of inference.

222 When we conducted pairwise comparisons, we found foraging behavior was lower in a group size
223 of 3 than in a group size of 2 ($t = 2.09$, $p = 0.04$) or 5 ($t = 2$, $p = 0.04$). We also found that locomotion was
224 higher at a group size of 4 compared to a group size of 2 ($t = 2.37$, $p = 0.02$) or 3 ($t = 2.31$, $p = 0.02$).
225 Social behavior was higher in a group size of 5 than in all four other group sizes (Table 4). Repetitive
226 behavior did not differ across group size for most elephants.

227

228 *3.4. Behavioral Differences Across Individual Subjects*

229 Since individual behavior can vary significantly and understanding variations in individual
230 behavior can be important for welfare, we assessed behavior status of individual elephants by testing for
231 the variance component of the random effect for subject, and found that all but social behavior differed
232 significantly ($p < 0.01$) between subjects. Test results are in A10. Male 1 and Female 3 displayed
233 repetitive behavior at a much higher frequency than the other individuals. Further, Male 2 and Female 3

234 had a higher frequency of resting behavior than other individuals. Female 1 and Female 2 - the two
235 youngest elephants in this study - displayed the most locomotion behavior (Figure 5).

236

237 **4. Discussion**

238

239 *4.1. Effect of diet changes across time of day*

240 Wild elephants spend a large portion of their day foraging (Wittemyer et al., 2007). In zoos,
241 foraging may decrease towards the end of the day as elephants exhaust existing resources (Mackey, 2014;
242 Stoinski et al., 2000). The NC Zoo feeds the elephants hay in the morning (~08:00) and evening (~16:00),
243 but does not provide a consistent meal midday. Reducing pelleted diet and increasing browse and hay
244 may help increase fiber and better simulate a natural diet for African elephants. While increasing browse
245 did not increase the total time spent foraging, it did lead to an increase in foraging behavior in the
246 afternoon ($t = 2.24$, $p = 0.03$) and supports previous work that showed alterations in diet can increase
247 foraging behavior in elephants (Björk, 2011; Greco et al., 2016; Morimura and Ueno, 1999; Stoinski et
248 al., 2000; Rees, 2009; Wilson et al., 2004). Using both a low inclusion diet and increasing browse appears
249 to have had a positive effect on elephant behavior and may allow zoos to increase food availability and
250 foraging opportunities without increasing total caloric intake.

251 Beyond foraging behavior, time of day also affected social, repetitive, locomotion, and resting
252 behavior. In other studies, behavior differed greatly across time of day due to major daily events,
253 especially around feeding times (Horback et al., 2014; Posta et al., 2013; Rees, 2009). Repetitive behavior
254 is negatively correlated with feeding behavior and increases in the afternoon prior to shifting elephants
255 (Hasenjager and Bergl, 2015; Rees, 2009). While we did find an increase in foraging behavior in the
256 afternoon after increasing the amount of browse provided to elephants, repetitive behavior was still more
257 common in the afternoon (i.e., when food availability was lowest). A lack of foraging material has been
258 found to have a significant effect on a variety of other behaviors in previous studies (Posta et al., 2013;

259 Rees, 2009). Similarly, increases in social and resting behavior observed from morning to afternoon may
260 also be related to reductions in forage availability that occur across time of day.

261 In this study, altering the diet of the individual elephants appears to have affected foraging
262 behavior, but was not sufficient to deter increases in repetitive behavior seen in the afternoon (although it
263 should be noted that repetitive behavior made up a small portion of overall activity budget regardless of
264 time of day). In addition to incorporation of more browse, using management options such as spreading
265 out food, using puzzle feeders, and varying feeding times, frequency, and location can increase the
266 amount of time and effort required for the elephants to obtain food (Lehnhardt, 2006; Meehan et al.,
267 2016b; Posta, 2011). Providing other forms of stimulation (i.e., enrichment, daily walks, or training
268 interactions with zookeepers) may be required to deter repetitive behavior at their peak times, often in the
269 afternoon (Greco et al., 2016; Meehan et al., 2016a,b). Finally, increasing unpredictability of the schedule
270 may further help to deter repetitive behaviors that are anticipatory (Mackey, 2014; Stoinski et al., 2000).

271

272 *4.2. Effects of group size and complexity*

273 Changes in social structure and herd complexity affected elephant behavior. Previous studies
274 have indicated that changes in housing situations and social groupings alter repetitive behavior (Meehan
275 et al., 2016a). Presence of juveniles, time spent outdoors, and limiting individual housing can decrease
276 repetitive behaviors. Furthermore, increasing elephant group size in captive environments can improve
277 welfare (Rees, 2009). Wild African elephant cows can live in groups anywhere from 8 - 100 individuals,
278 depending on the time of year (Wittemyer et al., 2007) and increasing group size in captive elephants
279 appears to improve welfare.

280 We observed more social behavior both when a male elephant was present and during
281 observations of the largest group size (n = 5). Variations of behavior across group size and composition
282 highlight the value of integrating African male elephants with females and the importance of increasing
283 group size in captive herds. While housing bulls with cows has traditionally been avoided in US zoos due
284 to concern of injury or restrictions on sexual behavior, our findings support the importance of integrating

285 bulls with the herd. In the wild, African elephant males can be solitary, but they are also found in bachelor
286 groups and intermingle with female family units during the mating season (Wittemyer et al., 2007). In this
287 study, social behavior increased for all elephants in larger group sizes, thus, multi-sex group management
288 may improve elephant welfare.

289 We found that group size and social behavior were significantly correlated when a male elephant
290 was present, however, this behavioral change included an increase in the observed affiliative as well as
291 agonistic behaviors being displayed. While all agonistic behaviors should not necessarily be considered
292 negative, it is important to consider the specific effects of increasing group size and complexity on overall
293 social experience. Unrelated wild elephants rarely intermingle since groups consist of matriarchal-led
294 family units (Wittemyer et al., 2007). Therefore, perhaps unsurprisingly, artificially-created groups of
295 zoo-housed elephants will need to establish new relationships in the herd structure with every new
296 introduction. Therefore, introduced elephants initially housed separately may undergo an initial
297 acclimation period that can possess higher rates of agonistic interaction. Zoos should provide an adequate
298 amount of time for new relationships to form, and we strongly suggest development of long-term studies
299 on *ex-situ* social introductions to better understand the acclimation period and overall effects of changes
300 in social group structure and complexity on elephant welfare. Furthermore, we also highly suggest zoos
301 supply adequate space for elephants to physically avoid each other during introductory periods. This can
302 allow elephants to avoid aggressive behaviors and provide individuals the choice to remove themselves
303 from unwanted social interaction. This provides elephants agency to make decisions, which is a crucial
304 element to support optimal welfare in zoo-housed animals (Greco et al., 2016; Hasenjager and Bergl
305 2015; Learmonth 2019; Mackey 2014; Meehan et al., 2016b). It should be noted that it is important to
306 ensure that the elephants are socially compatible, as chronic stress from living in an incompatible group
307 can significantly reduce welfare (Meehan et al., 2016a; Prado-Oviedo et al., 2016).

308

309 *4.3. Hormone cycle effects*

310 Hormonal stage of the elephant had notable effects on behavior. Female elephants increased
311 repetitive and social behaviors and decreased foraging behaviors during the follicular stage, while males
312 increased repetitive and resting behaviors and decreased foraging and social behaviors during musth.
313 Wild bulls dramatically increase their home range size and are often seen roaming over wide areas while
314 in musth (Wittemyer et al., 2007). It was therefore surprising that the bulls in this study did not increase
315 their locomotive activity and increased their resting behavior during musth in this study. The majority
316 (>99%) of resting behaviors observed in this study were standing rest versus reclined rest, and our lack of
317 distinction between standing rest and standing but not resting may have affected these results. However,
318 the increase in repetitive behaviors observed during musth could be a result of bulls having an inner drive
319 to increase their movements.

320 Affiliative behaviors were more prevalent in female elephants during the follicular stage.
321 Research suggests that females of primate species may increase social displays of behavior during
322 ovulation (van Schaik et al., 1999), and behavioral differences across hormonal cycles in elephants has
323 been observed in other studies as well (Slade-Cain et al., 2008). Thus, ovulation and female hormonal
324 cycling should be considered when managing individuals for optimal welfare, as social interactions were
325 more positive and more frequent during follicular stage. Changing group composition, introduction to
326 male elephants, or other social changes conducted when female elephants are in follicular stage could
327 promote positive social interactions.

328 Note, keepers only used visual indicators of musth and did not conduct hormonal testing for
329 testosterone levels in bulls. While lack of hormonal testing for testosterone levels may limit how musth
330 can be quantified, we feel that for the purposes of our study visual indicators were sufficient to look at
331 changes in behavior when in or not in musth.

332

333 *4.4. Individual Behavioral Differences*

334 Elephants are cognitively complex, so researchers often find value in examining individual
335 behavior when evaluating overall behavioral patterns (Holdgate et al., 2016; Horback et al., 2014; Mason

336 and Veasey, 2010; Meehan et al., 2016b; Posta, 2011; Posta et al., 2013; Rees, 2009; Stoinski et al., 2000;
337 Vanitha et al., 2011; Veasey, 2006). African elephants display individual personalities and certain life
338 traits (i.e., age, sex, etc.) can lead to individual variation in behavior (Grand et al., 2012; Holdgate et al.,
339 2016; Horback et al., 2013; Horback et al., 2014; Lee and Moss, 2012; Mason and Veasey, 2010; Meehan
340 et al., 2016b; Posta, 2011; Posta et al., 2013; Rees, 2009; Stoinski et al., 2000; Vanitha et al., 2011;
341 Veasey, 2006; Yasui, 2013). Wild female elephants have been known to exhibit personality traits
342 associated with certain leadership and social integration abilities (Yasui et al., 2013). Such traits can
343 influence how individuals interact with their environment and with conspecifics, and accounting for
344 individual variation for elephant management is arguably necessary.

345 Male 2, the oldest elephant at the NC Zoo, followed by Female 3, displayed the highest amounts
346 of resting behavior. Both of these elephants exhibited multiple foot lesions and gait abnormalities
347 throughout the study period, which could have led to this higher frequency of resting behavior. The
348 majority (>99%) of all resting behavior observed by elephants was standing rest (versus resting – lying
349 down). Zoo elephants possess a high rate of degenerative joint disease and foot lesions (Miller et al.,
350 2016), which may contribute to the predilection for rest in older elephants seen in this study. Monitoring
351 foot and gait issues in zoo elephants has been marked as important in previous studies (Miller et al.,
352 2016), and we can specifically highlight how these chronic issues may have an effect on the elephant's
353 locomotion behavior and, potentially, physical health due to the lack of movement associated with higher
354 rest in elephants with chronic issues.

355 Female 1 and Female 2, the zoo's two youngest elephants, displayed the most locomotive
356 behavior. Older individuals, regardless of species, diet, or physical fitness, usually rest more due to the
357 difficulties in movement that come with age. Male 1, the younger of the two bulls, is a more active
358 individual, which may have caused the individual to influence female behavior differently than how Male
359 2 influenced female behavior. Younger individuals display play behavior more frequently than older
360 counterparts (Bekoff and Byers, 1998) and their presence can cause decreased repetitive and increased
361 social behavior across captive groups (Troxell-Smith et al., 2017; Webber and Lee 2020). Since Female 1

362 or Female 2 was always present in a group size larger than 2, we are unable to know for sure whether
363 their presence caused changes in behavior or if it was the size of the group itself. However, their presence
364 may potentially positively alter the behavior of the other elephants within the exhibit. All but one
365 individual included in this study are considered adults so we weren't able to assess the effect of age on
366 behavior, but this is likely to be an important factor in overall elephant behavior.

367

368 **5. Conclusion**

369 Elephant behavior is affected by both environmental conditions and managerial decisions, and
370 studies need to consider the interactions of numerous variables to fully understand the patterns.
371 Specifically, managers should concentrate on increasing positive and decreasing negative behaviors while
372 recognizing that these may have natural variation with time of day and are affected by individual history
373 and hormone status. Overall, we provide evidence that increasing browse improves opportunities for
374 foraging behavior, particularly in the afternoon, but was not sufficient to reduce repetitive behaviors.
375 Other management techniques will be needed to reduce repetitive behaviors particularly when foraging
376 materials are lacking (Greco et al., 2016; Meehan et al., 2016b). Repetitive behaviors are complex
377 behaviors which, once developed, are difficult to extinguish (Björk, 2009; Wilson and Bloomsmith,
378 2004). Repetitive behaviors are suggestive of one or more underlying stressors, and until the perceived
379 stress is removed, it is unlikely that the stereotypy will cease (Björk, 2009; Wilson and Bloomsmith,
380 2004).

381 Increasing group size and integrating bulls with cows had a positive impact on elephant welfare.
382 In addition, forming male-female groups may act as a deterrent for agonistic behaviors between female
383 elephants, leading to a more optimal group dynamic. Our data suggest that because social behavior is
384 elevated in the follicular phase, this may be the ideal time to alter herd structure or conduct introductions
385 in order to promote positive interactions. While we found no negative implications of introductions or
386 altering group structure, studies analyzing indicators of stress and complexity in zoo-housed elephant
387 herds may be warranted to improve our understanding of the costs and benefits of herd manipulation.

388 Finally, zoos should consider significant differences exist among individual elephant's behavioral patterns
389 and individual history and personality when managing elephants in their care. In addition to our findings,
390 we note that it is crucial for zoos to allow agency for elephants, providing them choices in management
391 decisions whenever possible (Greco et al., 2016; Hasenjager and Bergl 2015; Learmonth 2019; Mackey
392 2014; Meehan et al., 2016b).

393

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399

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560

561 **Tables**

562 **Table 1.** Akaike's Information Criteria (AIC) and generalized chi-square statistics from generalized
563 linear models with and without random observer effects.

Response	Chisq	df	AICC with observer effect	AICC without observer effect
Foraging	5.53	5.64	2236.39	2251
Locomotion	1.44	1.57	964.88	985.41
Resting	5.88	7.06	2935.54	3329.33
Social	2.41	3.17	2045.02	2222.03
Repetitive	5.34	6.19	3480.75	3723.24

564

565 **Table 2.** F-tests for factorial effects of time-of-day and diet change on behavior frequencies.

Behavior	Effect	DF	Den DF	F Value	Prob F
Foraging	Diet_Change	1	376	0.22	0.6378
Foraging	Time_of_Day	2	376	198.51	<.0001
Foraging	Diet_Change * Time_of_Day	2	376	2.69	0.0692
Locomotion	Diet_Change	1	376	0.06	0.8021
Locomotion	Time_of_Day	2	376	4.39	0.013
Locomotion	Diet_Change * Time_of_Day	2	376	0.44	0.6459
Resting	Diet_Change	1	376	0.01	0.9277
Resting	Time_of_Day	2	376	122.77	<.0001
Resting	Diet_Change * Time_of_Day	2	376	0.39	0.6752
Social	Diet_Change	1	376	0.03	0.8546
Social	Time_of_Day	2	376	9.25	0.0001
Social	Diet_Change * Time_of_Day	2	376	3.2	0.0419
Repetitive	Diet_Change	1	376	1.89	0.1698
Repetitive	Time_of_Day	2	376	88.56	<.0001
Repetitive	Diet_Change * Time_of_Day	2	376	0.34	0.7126

566

567 **Table 3.** F-tests for hormone effects from generalized linear models for each behavioral category.

Behavior	Sex	DF	Den DF	F Value	Prob F
Foraging	Female	1	254	22.38	<.0001
Foraging	Male	1	254	24.2	<.0001
Locomotion	Female	1	254	0.06	0.7995
Locomotion	Male	1	254	0.26	0.6113
Resting	Female	1	254	0	0.9585
Resting	Male	1	254	26.96	<.0001
Social	Female	1	254	12.07	0.0006
Social	Male	1	254	4.36	0.0378
Repetitive	Female	1	254	53.91	<.0001
Repetitive	Male	1	254	4.08	0.0445

568

569

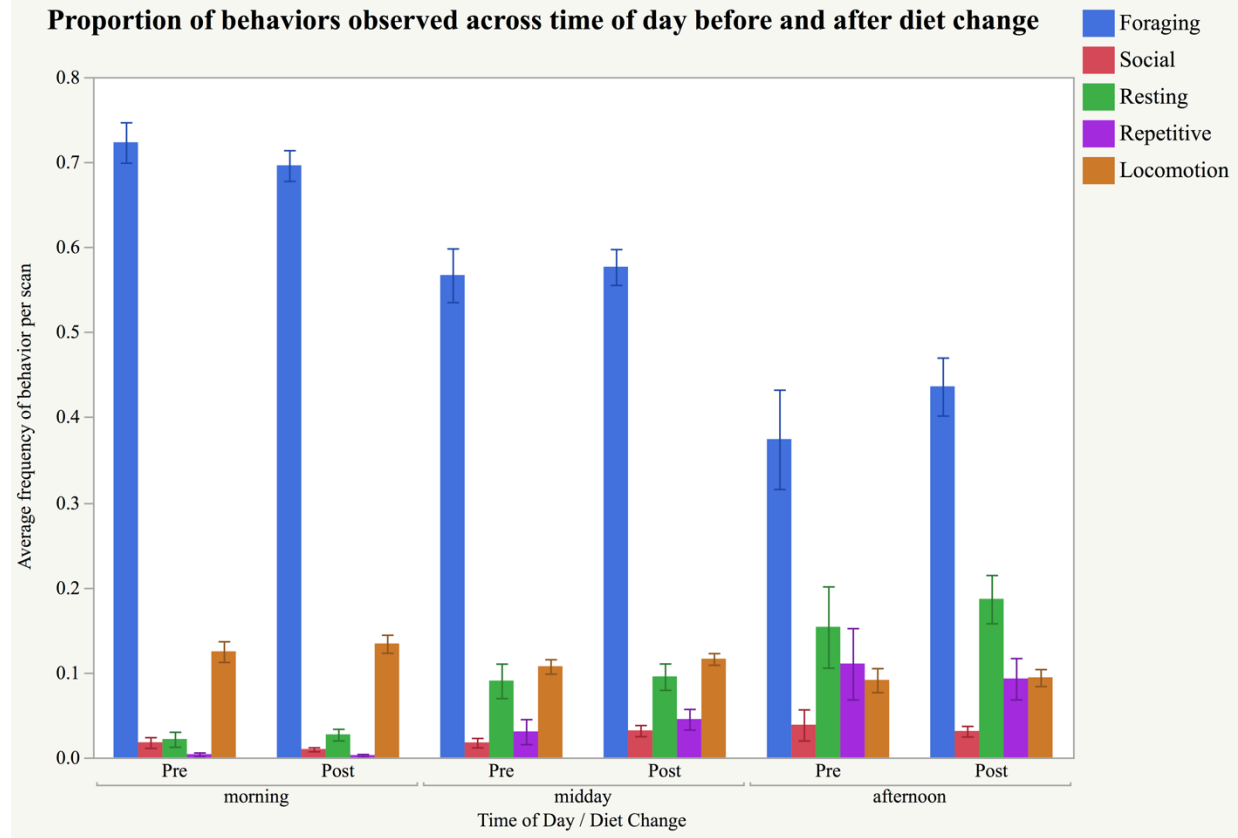
Table 4. F-tests analyzing how group size affects elephant behavior.

Behavior	F Value	Prob F
Foraging	2.01	0.0924
Locomotion	2.39	0.0506
Resting	2.34	0.0544
Social	4.46	0.0016
Repetitive	1.31	0.2668

570

571

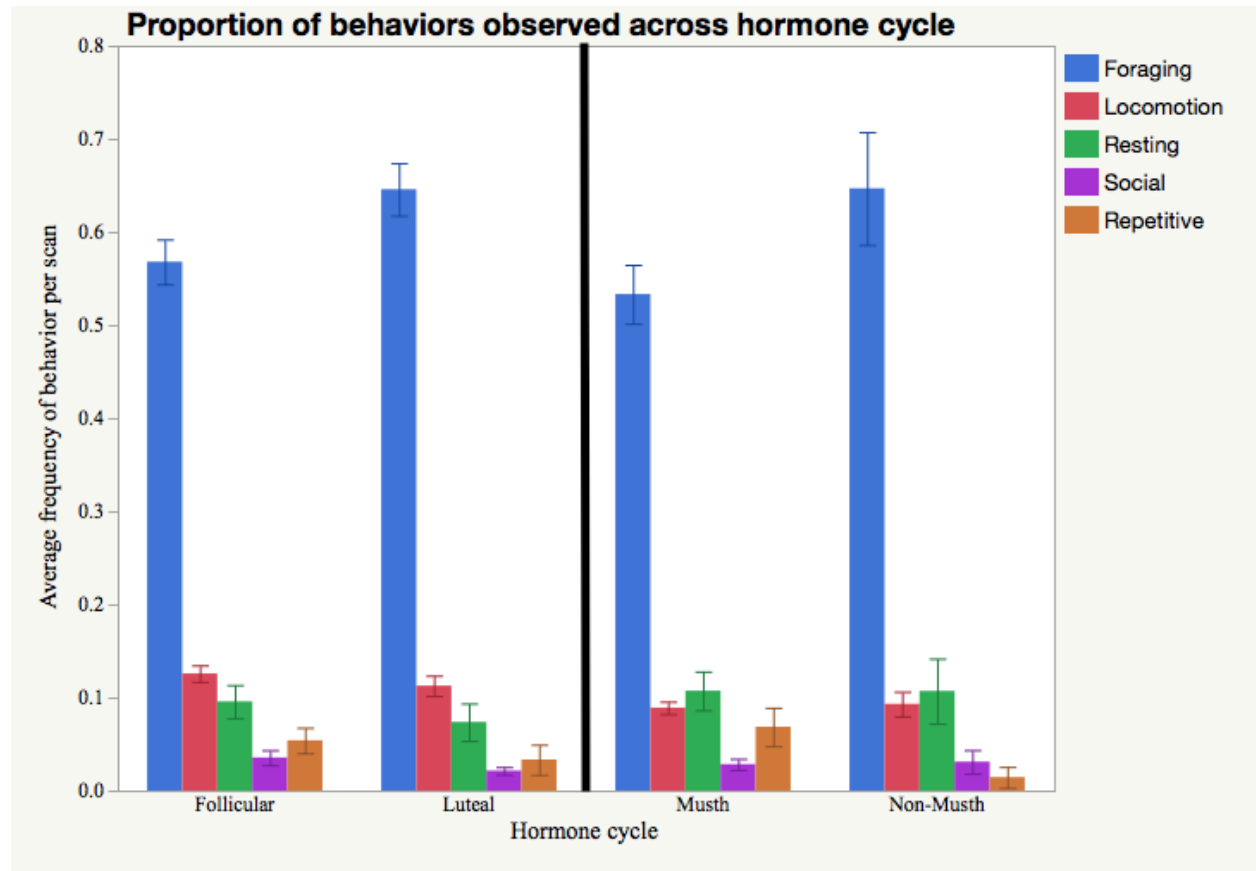
572 **Figures**



573

574 **Figure 1.** Pattern of behaviors displayed with respect to time of day before and after the change in diet.

575

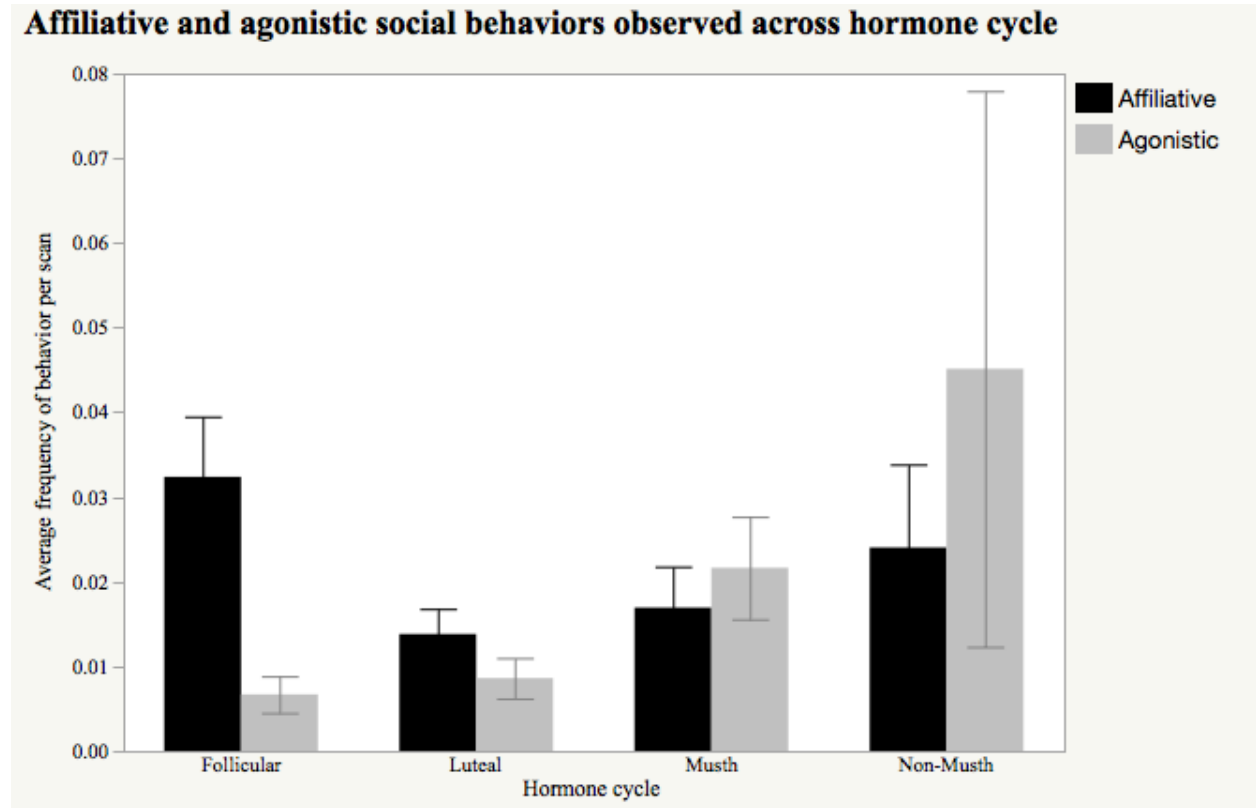


576

577 **Figure 2.** The proportion of behaviors displayed across hormonal cycle for female (follicular and luteal)

578 and male (musth and non-musth) elephants.

579



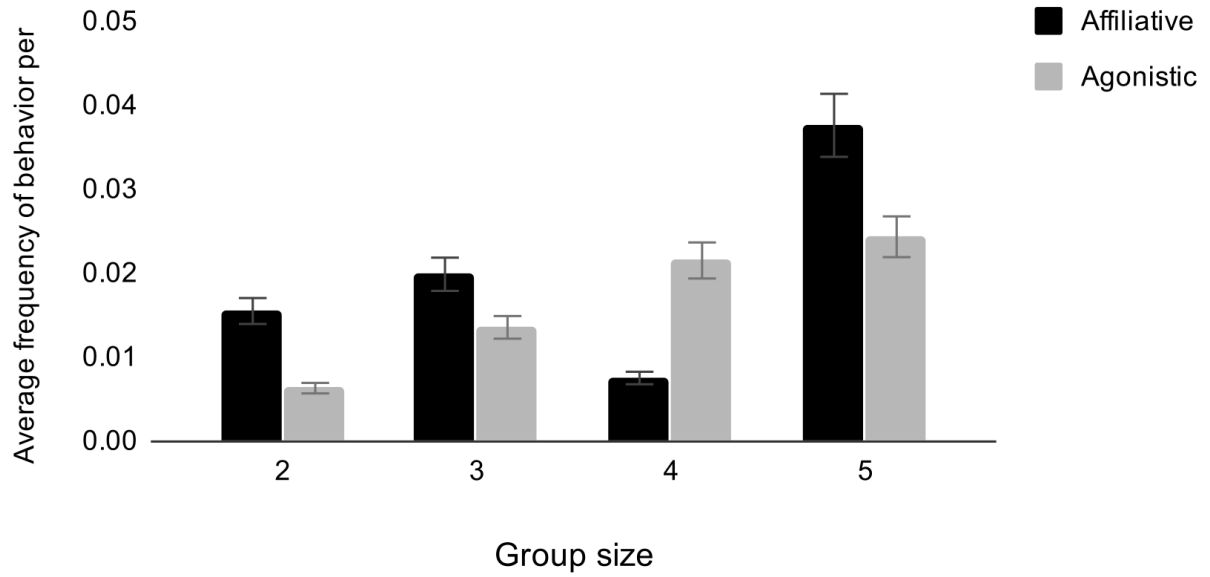
580

581 **Figure 3.** Differences in affiliative (positive) and agonistic (negative) behaviors across male and female

582 elephant hormone cycles.

583

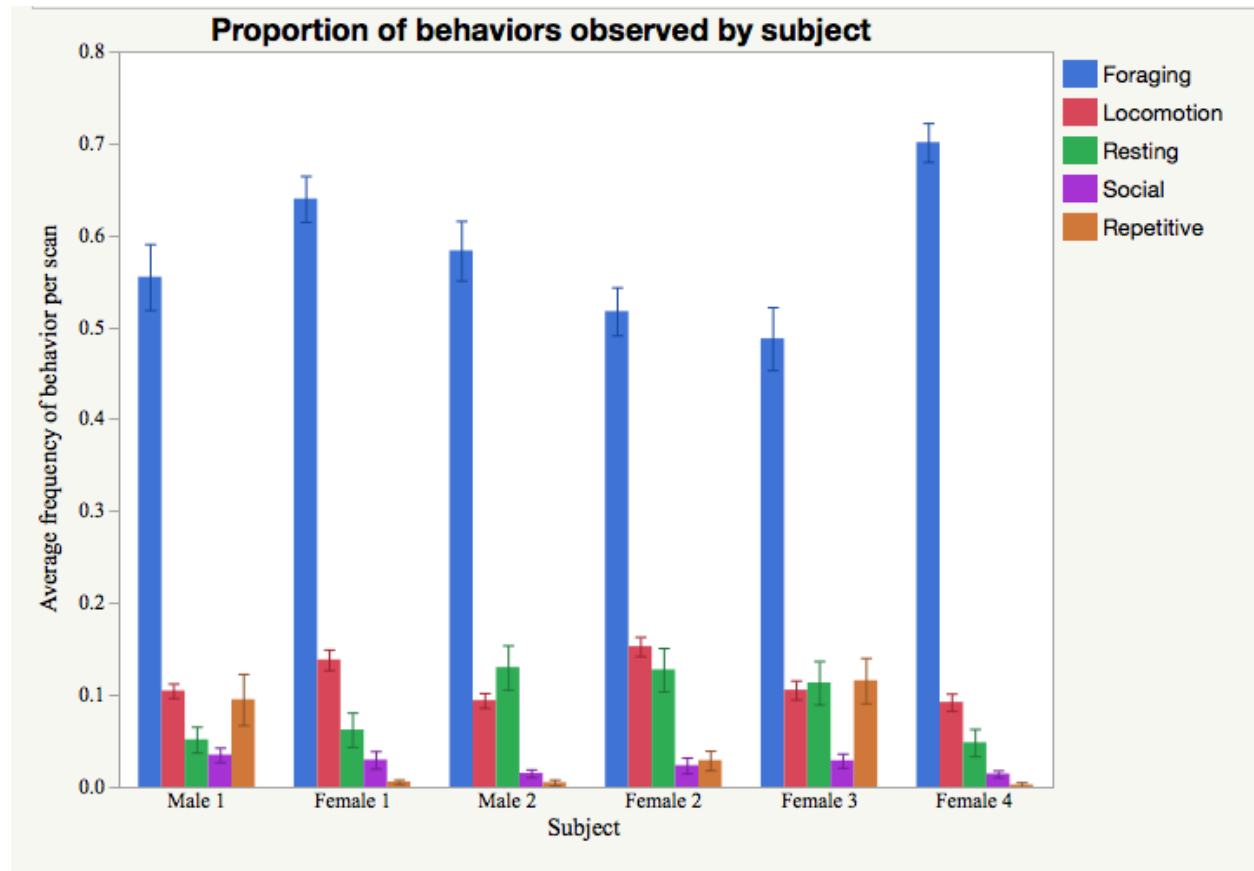
Affiliative and agonistic social behaviors observed across group size



584

585 **Figure 4.** Frequency of behaviors displayed for each group size.

586



587

588 **Figure 5.** Frequency of behaviors displayed by all individual elephants in the study.

589

590 **Appendix 1**591 **Table A1.** Ethogram used in behavioral observations of elephants.

Behavior	Description
Self-Maintenance	Rubbing, scratching, throwing sand/dirt/hay/water/fecal material onto body, mudding, dusting, or digging.
Resting – Standing	No interactions with conspecifics, environment, or keepers; no bodily movement. Can be asleep or awake, while maintaining an upright position, supported by feet.
Resting – Lying down	Position in which the elephant's body is flat on the ground, and the animal appears to be sleeping or resting. No bodily movement apparent.

Resting – partial	Animal’s body is lying on ground, but head still be upright. No bodily movement apparent.
Resting – Stretch	Elephant supports itself on its knees and elbows with rear legs extended back and front legs extended forward.
Pacing	Walking or running back and forth between point A and B or in a circle. May include eating.
Rocking	Swaying back and forth with no locomotion. May include eating.
Other Repetitive Behavior	Other recurrent behavior whose cause and function are unknown. May include eating.
Locomotion	Walking or running non-repetitively.
Spinning	Elephant turns in circle repetitively.
Vocalization	Elephant makes an audible sound.
Forage – Exhibit Vegetation	Browsing on trees/shrubs/grass.
Forage – Prepared Diet	Eating prepared diet (hay/grain/vegetables).
Forage – Browse	Eating cut browse.
Forage - Sand	Eating sand.
Drinking	Drinking from a pool or drinker.
Interacting – Exhibit Structure	Interacting with permanent exhibit structures. Does not include eating.
Interacting – Fencing	Touching or manipulating with cage bars/fencing, both on- and off-exhibit.

Interacting – Temporary Enrichment	Manipulating any temporary non-food enrichment items, such as tires or barrels.
Bathe	Bathing in exhibit pond. Does not include splashing water while standing at the pool edge.
Other Solitary Behavior	Other solitary behaviors (e.g. moving trunk, defecating, etc.).
Agonistic – Non- Contact	Threats (ears extended, charging, head shake, pursuit). No physical contact between individuals.
Agonistic – Contact	Aggressive behavior involving physical contact between individuals; can include biting, head-butting, poking, striking with the trunk, or pushes.
Affiliative – Contact	Behaviors that involve any non-aggressive physical contact; includes trunk intertwining, trunk placed within another elephant’s mouth, contact with another elephant without obvious use of force.
Displace	Focal elephant approaches another elephant which then leaves its position; the focal elephant takes up the vacant position.
Displaced	Focal elephant moves from its position as another elephant approaches it; the other elephant then takes up the vacant position.
Keeper Interaction	Interacting with a keeper.
Not Visible	Elephant or its behavior is not visible to the observer.
Other	Elephant engages in any behavior that does not meet the above behaviors.

592

593 **Table A2.** Observation budgets of each elephants within social groups, pre-diet change, and post-diet
594 change.

Subject	Observations by Group ID*	Observations by Diet Change	Total # Observations
----------------	----------------------------------	--	---------------------------------

33 Lasky

	<i>1</i>	<i>3</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>10</i>	<i>11</i>	<i>12</i>	<i>16</i>	<i>Pre-Diet Change</i>	<i>Post-Diet Change</i>	
Male 1	636	1082								604	1114	1718
Male 2	90	90	313	115	60		205	1105		569	1409	1978
Female 1		1261	144	60	199	316				693	1287	1980
Female 2			261		140			1144	317	430	1432	1862
Female 3			229		231			1085	405	546	1404	1950
Female 4		983	205	60	199	395		60		610	1292	1902

595

596 ***Group IDs:**

Group ID	Individuals in Group
1	Male 1
3	Male 1, Female 1, Female 4
6	Female 1, Male 2, Female 2, Female 3, Female 4
7	Female 1, Male 2, Female 4
8	Female 1, Female 2, Female 3, Female 4
10	Female 1, Female 4
11	Male 2
12	Male 2, Female 2, Female 3
16	Female 2, Female 3

597