

## Supplementary Materials

### Social behavior and group formation in male Asian elephants (*Elephas maximus*): The effects of age and musth in wild and zoo-housed animals

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**Table S1.** List of candidate models used during linear mixed model (LMM) approach to identify factors (including potentially interacting effects) that contributed to variation in the rate of social behaviors (aggression, prosocial behavior, dominance behavior, submissive behavior). Models were constructed separately for each behavior, and for wild and zoo-housed elephants. All models included focal animal identity as a random factor.

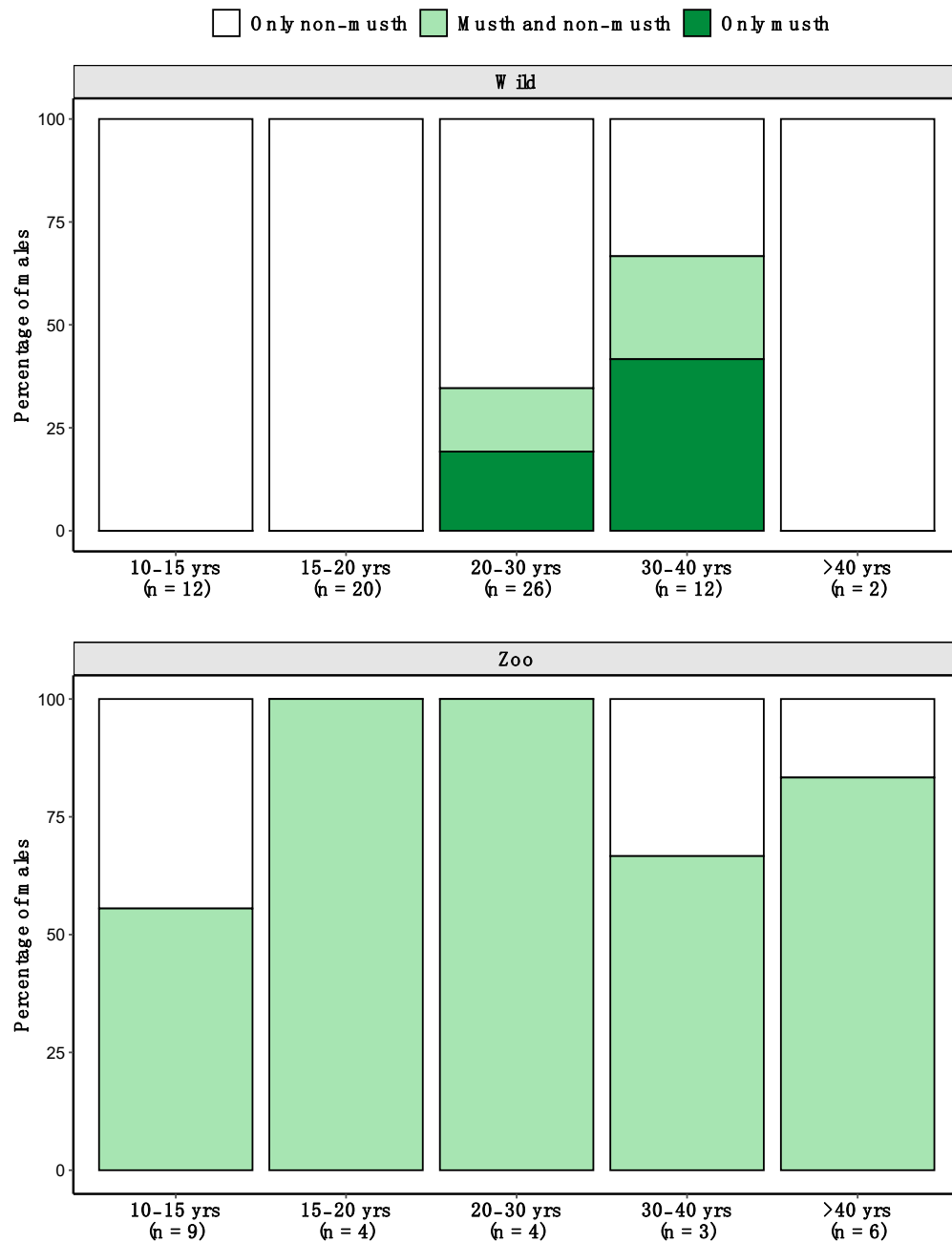
No.	Model structure
1	Behavior rate ~ Null
2	Behavior rate ~ Musth status <sup>†</sup>
3	Behavior rate ~ Musth status + Age <sup>‡</sup>
4	Behavior rate ~ Musth status × Age
5	Behavior rate ~ Musth status + Age + Group type <sup>§</sup>
6	Behavior rate ~ Musth status × Age × Group type
7	Behavior rate ~ Musth status + Age + Group type + Elephants present <sup>¶</sup>
8	Behavior rate ~ Musth status × Age × Group type + Elephants present
9	Behavior rate ~ Age
10	Behavior rate ~ Age + Group type
11	Behavior rate ~ Age × Group type
12	Behavior rate ~ Age + Group type + Elephants present
13	Behavior rate ~ Age × Group type + Elephants present

<sup>†</sup> Categorical variable: Non-musth (reference value), Early musth, Full musth, or Post-musth

<sup>‡</sup> Age class for wild elephants, and age in years for zoo-housed elephants

<sup>§</sup> Categorical variable: All-male group (reference value) or Mixed-sex group

<sup>¶</sup> Number of elephants present in same group during observation



**Figure S1.** Percentage of male Asian elephants in Wasgamuwa National Park, Sri Lanka (top panel), and in US zoos (bottom panel) of various age classes that were sighted in and/or out of musth over the study period (wild elephants, December 2018 to April 2019; zoo elephants, July 2018 to April 2021). The number of unique males in each age class are given on the horizontal axis. Each male is represented only once.

**Table S2.** Ranked regression models investigating effect of various factors on rates of social behavior in zoo-housed elephants. Other statistics include parameterization ( $k$ ), log-likelihood (LL), Akaike's Information Criterion score (AIC<sub>c</sub>), differences in AIC<sub>c</sub> ( $\Delta$ AIC<sub>c</sub>), Akaike weight ( $w_i$ ), and cumulative Akaike weights (cum.  $w_i$ ) calculated with restricted maximum likelihood estimation. Refer to Table S1 for descriptions of each parameter. Asterices (\*) indicate term(s) from the best model that were dropped for non-significance in the "best" model; marginal coefficients of determination ( $R^2_c$ ) are given for the best model after non-significant term(s) were dropped.

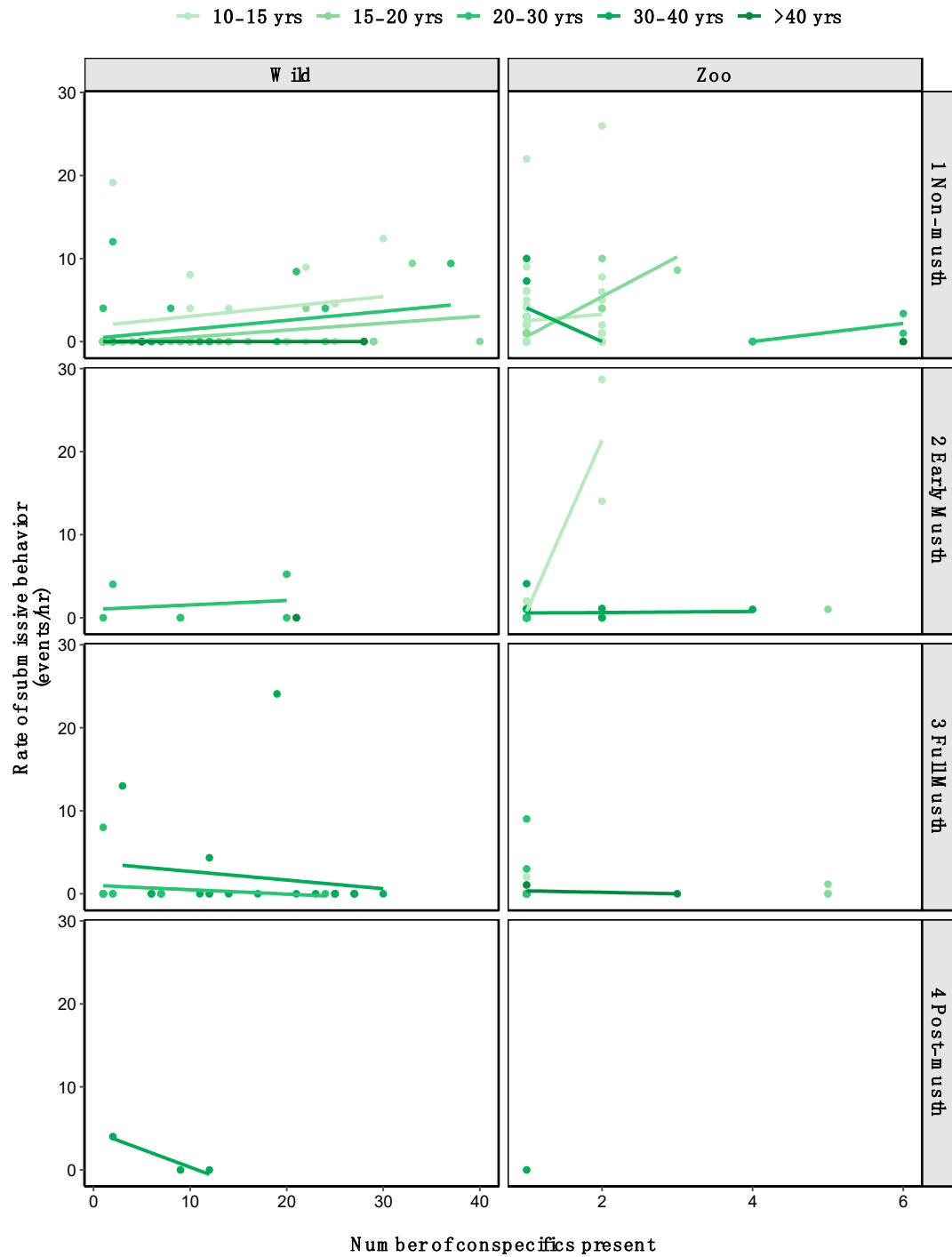
Zoo elephants: Rates of social behavior	$k$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$	LL	cum. $w_i$
<b>Aggression: <math>R^2_c = 0.142</math></b>						
Age × Group type	6	741.19	0.00	0.17	−364.26	0.17
Age + Group type	5	741.40	0.20	0.15	−365.46	0.32
Age × Group type + Elephants present	7	741.81	0.62	0.12	−363.46	0.44
Age + Group type + Elephants present	6	742.03	0.84	0.11	−364.68	0.55
Age	4	742.20	1.01	0.10	−366.94	0.65
Null (intercept only)	3	742.85	1.66	0.07	−368.33	0.72
Musth status × Age × Group type	15	743.18	1.98	0.06	−354.52	0.78
Musth status + Age + Group type	8	743.39	2.20	0.06	−363.11	0.84
Musth status + Age + Group type + Elephants present	9	743.68	2.48	0.05	−362.10	0.89
Musth status × Age × Group type + Elephants present	16	743.72	2.53	0.05	−353.50	0.94
Musth status × Age	9	744.58	3.39	0.03	−362.55	0.97
Musth status + Age	7	744.81	3.62	0.03	−364.95	0.99
Musth status	6	747.54	6.35	0.01	−367.43	1.00
<b>Prosocial behavior: <math>R^2_c = 0.476</math></b>						
Musth status × Age × Group type + Elephants present	16	950.70	0.00	1.00	−456.99	1.00
Musth status + Age + Group type + Elephants present	9	965.09	14.39	0.00	−472.81	1.00
Age + Group type + Elephants present	6	969.87	19.16	0.00	−478.60	1.00
Musth status × Age × Group type	15	971.49	20.79	0.00	−468.68	1.00
Age × Group type + Elephants present	7	971.70	20.99	0.00	−478.40	1.00
Musth status × Age	9	983.14	32.44	0.00	−481.83	1.00
Age	4	983.94	33.23	0.00	−487.81	1.00
Null (intercept only)	3	984.82	34.12	0.00	−489.32	1.00
Age + Group type	5	985.52	34.81	0.00	−487.52	1.00
Musth status + Age	7	985.88	35.17	0.00	−485.49	1.00
Musth status + Age + Group type	8	986.86	36.15	0.00	−484.84	1.00
Age × Group type	6	987.56	36.85	0.00	−487.44	1.00
Musth status	6	989.72	39.01	0.00	−488.52	1.00
<b>Dominance behavior: <math>R^2_c = 0.007</math></b>						

Null (intercept only)	3	787.81	0.00	0.37	-390.81	0.37
Age	4	789.16	1.35	0.19	-390.42	0.56
Musth status	6	789.51	1.70	0.16	-388.42	0.72
Age + Group type	5	791.18	3.37	0.07	-390.35	0.79
Musth status + Age	7	791.57	3.76	0.06	-388.33	0.85
Age + Group type + Elephants present	6	792.21	4.40	0.04	-389.77	0.89
Age × Group type	6	792.46	4.65	0.04	-389.89	0.93
Age × Group type + Elephants present	7	793.52	5.71	0.02	-389.31	0.95
Musth status + Age + Group type	8	793.76	5.95	0.02	-388.29	0.97
Musth status × Age	9	794.02	6.21	0.02	-387.27	0.98
Musth status + Age + Group type + Elephants present	9	794.16	6.35	0.02	-387.34	1.00
Musth status × Age × Group type + Elephants present	16	803.69	15.88	0.00	-383.48	1.00
Musth status × Age × Group type	15	805.00	17.19	0.00	-385.43	1.00
<b>Submissive behavior: <math>R^2_c = 0.276</math></b>						
Musth status × Age × Group type + Elephants present*	16	756.07	0.00	0.52	-359.67	0.52
Musth status × Age × Group type	15	756.51	0.44	0.42	-361.19	0.94
Age + Group type + Elephants present	6	762.75	6.68	0.02	-375.04	0.96
Age + Group type	5	762.82	6.74	0.02	-376.17	0.98
Age × Group type + Elephants present	7	764.14	8.07	0.01	-374.62	0.99
Age × Group type	6	764.18	8.10	0.01	-375.75	1.00
Age	4	768.25	12.18	0.00	-379.97	1.00
Musth status + Age + Group type + Elephants present	9	768.58	12.51	0.00	-374.55	1.00
Musth status + Age + Group type	8	768.99	12.92	0.00	-375.91	1.00
Null (intercept only)	3	771.20	15.13	0.00	-382.51	1.00
Musth status + Age	7	774.09	18.02	0.00	-379.59	1.00
Musth status	6	776.09	20.01	0.00	-381.71	1.00
Musth status × Age	9	776.36	20.28	0.00	-378.44	1.00

**Table S3.** Ranked regression models investigating effect of various factors on rates of social behavior in wild elephants. Other statistics include parameterization ( $k$ ), log-likelihood (LL), Akaike's Information Criterion score (AIC<sub>c</sub>), differences in AIC<sub>c</sub> ( $\Delta$ AIC<sub>c</sub>), Akaike weight ( $w_i$ ), and cumulative Akaike weights (cum.  $w_i$ ) calculated with restricted maximum likelihood estimation. Refer to Table S1 for descriptions of each parameter. Asterisks (\*) indicate term(s) from the best model that were dropped for non-significance in the "best" model; marginal coefficients of determination ( $R^2_c$ ) are given for the best model after non-significant term(s) were dropped.

<b>Wild elephants: Rates of social behavior</b>	$k$	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$	LL	cum. $w_i$
<b>Aggression: <math>R^2_c = 0.371</math></b>						
Age + Group type* + Elephants present*	9	363.73	0.00	0.52	-172.15	0.52
Age	7	364.92	1.18	0.29	-175.02	0.80
Age + Group type	8	367.16	3.43	0.09	-175.01	0.90
Null (intercept only)	3	368.01	4.28	0.06	-180.92	0.96
Musth status + Age + Group type + Elephants present	12	370.62	6.89	0.02	-172.04	0.97
Musth status + Age	10	371.80	8.07	0.01	-175.02	0.98
Age × Group type + Elephants present	13	371.84	8.11	0.01	-171.43	0.99
Musth status	6	373.60	9.86	0.00	-180.47	0.99
Musth status + Age + Group type	11	374.15	10.42	0.00	-175.01	1.00
Age × Group type	12	374.85	11.12	0.00	-174.16	1.00
Musth status × Age	13	379.00	15.27	0.00	-175.01	1.00
Musth status × Age × Group type + Elephants present	21	392.48	28.75	0.00	-171.19	1.00
Musth status × Age × Group type	20	395.53	31.80	0.00	-174.11	1.00
<b>Prosocial behavior: <math>R^2_c = 0.239</math></b>						
Age + Group type + Elephants present	9	1078.14	0.00	0.89	-529.35	0.89
Musth status + Age + Group type + Elephants present	12	1082.99	4.85	0.08	-528.22	0.96
Age × Group type + Elephants present	13	1084.65	6.52	0.03	-527.83	1.00
Age + Group type	8	1092.43	14.29	0.00	-537.65	1.00
Null (intercept only)	3	1094.07	15.93	0.00	-543.94	1.00
Musth status + Age + Group type	11	1096.87	18.73	0.00	-536.37	1.00
Musth status	6	1097.50	19.36	0.00	-542.42	1.00
Age × Group type	12	1098.34	20.20	0.00	-535.90	1.00
Musth status × Age × Group type + Elephants present	21	1100.92	22.79	0.00	-525.41	1.00
Age	7	1102.15	24.01	0.00	-543.64	1.00
Musth status + Age	10	1105.31	27.17	0.00	-541.77	1.00
Musth status × Age	13	1109.24	31.10	0.00	-540.13	1.00
Musth status × Age × Group type	20	1113.75	35.61	0.00	-533.22	1.00
<b>Dominance behavior: <math>R^2_c = 0.000</math></b>						

Null (intercept only)	3	812.00	0.00	0.81	-402.91	0.81
Age	7	817.01	5.01	0.07	-401.07	0.88
Musth status	6	817.18	5.18	0.06	-402.26	0.94
Age + Group type	8	819.02	7.02	0.02	-400.94	0.96
Musth status + Age	10	819.59	7.59	0.02	-398.92	0.98
Age + Group type + Elephants present	9	821.20	9.20	0.01	-400.88	0.99
Musth status + Age + Group type	11	821.54	9.54	0.01	-398.71	0.99
Musth status + Age + Group type + Elephants present	12	823.90	11.90	0.00	-398.68	1.00
Musth status × Age	13	824.45	12.45	0.00	-397.73	1.00
Age × Group type	12	825.01	13.01	0.00	-399.23	1.00
Age × Group type + Elephants present	13	827.39	15.39	0.00	-399.20	1.00
Musth status × Age × Group type	20	836.00	24.00	0.00	-394.35	1.00
Musth status × Age × Group type + Elephants present	21	838.71	26.71	0.00	-394.30	1.00
<b>Submissive behavior: <math>R^2_c = 0.121</math></b>						
Null (intercept only)	3	743.64	0.00	0.41	-368.73	0.41
Age + Group type + Elephants present	9	744.99	1.35	0.21	-362.78	0.62
Age	7	745.04	1.40	0.20	-365.08	0.82
Age + Group type	8	746.25	2.61	0.11	-364.56	0.93
Musth status	6	749.50	5.86	0.02	-368.42	0.95
Age × Group type + Elephants present	13	749.81	6.17	0.02	-360.41	0.97
Age × Group type	12	750.86	7.22	0.01	-362.16	0.98
Musth status + Age	10	751.61	7.97	0.01	-364.92	0.99
Musth status + Age + Group type + Elephants present	12	751.77	8.13	0.01	-362.62	1.00
Musth status + Age + Group type	11	752.92	9.28	0.00	-364.39	1.00
Musth status × Age	13	756.25	12.61	0.00	-363.63	1.00
Musth status × Age × Group type + Elephants present	21	768.85	25.21	0.00	-359.37	1.00
Musth status × Age × Group type	20	769.39	25.75	0.00	-361.04	1.00



**Figure S2.** Relationship between rates of submissive behavior and the number of conspecifics present during, for wild and zoo-housed male Asian elephants. Closed circles represent individual observation sessions, with regression lines shown for each age class (darker shades represent older age classes). Absence of a regression line for an age class indicates lack of adequate data for construction of a relationship. Note difference in scale on horizontal axis for wild and zoo-housed elephants.