Behavioral characterization of musth in Asian elephants (*Elephas maximus*): Defining progressive stages of male sexual behavior in *in-situ* and *ex-situ* populations

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ABSTRACT

Complementary studies of wild and zoo-housed animals offer insight into behavioral variation across a range of conditions including the context under which various behaviors evolved in natural settings. This information can be used to improve the sustainability of *in-situ* and *ex-situ* populations and enhance the well-being of individuals. Managed *ex-situ* populations are critical to the long-term existence of Asian elephants, yet relatively little is known about male reproductive behavior compared to females. Male elephants undergo a unique sexual state called "musth" that further complicates *in-situ* and *ex-situ* management strategies. The ability to manage musth males to enhance breeding success and overall wellness of elephants is dependent upon better understanding how intrinsic and extrinsic factors influence male behavioral variation around musth. Here, we observed 62 free-ranging male Asian elephants in Sri Lanka and compared their behavior to observations from 26 elephants managed in facilities around the US. We hypothesized that musth is associated with significant behavioral changes that can be used to define distinct stages in the progression of musth. During observations, we quantified environmental variables and recorded musth status of each focal elephant using visual indicators (temporal gland secretions and urine dribbling). We showed that musth's behavioral correlates (including changes in locomotion, foraging, alertness, and chemosensory behavior) were remarkably similar in wild and zoo-housed elephants. We also found that behavioral variation around musth was also associated with intrinsic (e.g., musth stage, age) and extrinsic factors (e.g., space availability, temperature) in zoo-housed, but not wild, elephants, indicating that musth is potentially plastic in changing environments. As musth progressed, we noted distinct behavioral signatures that define four stages of sexual activity in male elephants: non-musth, early musth, full musth, and post-musth. Finally, although we did not observe significant changes in overall social behavior (including aggression) during musth, we found that elephants increased the frequency with which they displayed certain behaviors associated with communication (e.g., alertness, chemosensory behavior, ear-flapping) in both populations. Together, these results indicate the significant behavioral changes that occur during musth in wild and zoo-housed elephants, and that musth progresses in distinct behavioral stages that can be easily distinguished by visual indicators. Studies like these serve to provide wildlife managers with information about a species' unique, evolved behavioral strategies and how these seemingly fixed behaviors may be influenced by intrinsic and extrinsic factors in predictable ways.

1. Introduction

The sustainability of many *ex-situ* mammal populations is threatened by challenges including breeding, the constraints of artificial environments, and individual animal welfare (Kleiman, 1994; Clubb and Mason, 2003; Mason, 2010). Many of these difficulties also jeopardize *in-situ* populations, and the complementary investigation of free-ranging and zoo-housed animals (including those in private parks and similar

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facilities) can lend insight into potential solutions for these problems, especially as the distinction between these populations becomes increasingly blurred (Clubb and Mason, 2007). For example, knowledge of the social organization of a threatened species can be used to form species-appropriate groups in human care (Swaisgood and Schulte, 2010; Schulte-Hostedde and Mastromonaco, 2015), and in turn the reproductive physiology of a species can be ascertained in the more controlled settings of zoos (Schwarzenberger and Brown, 2013). In striving to enhance the well-being of managed populations, wild populations can be used as a guide—not necessarily an imperative—to inform individual- and population-level management strategies (Mason and Veasey, 2010; McPhee and Carlstead, 2010).

Elephants, experience *in-situ* and *ex-situ* sustainability issues; Asian elephants (*Elephas maximus*) are endangered in the wild (Williams et al., 2020), and the captive North American population is unsustainable in the long-term predominantly due to a low number of reproductively active individuals (Nordin, 2017). Both populations have benefitted from complementary research between these groups (Schulte et al., 2007; Bechert et al., 2019; Conley, 2019; LaDue, 2019). For example, findings from *in-situ* and *ex-situ* elephant populations have helped to reveal elephants' unique reproductive physiology (Wasser et al., 1996; Brown et al., 1999; Freeman et al., 2011; Brown, 2014), and ongoing work serves to address the fatal elephant endotheliotropic herpesvirus that threatens both wild and zoo-housed elephants (Richman et al., 1999; Long et al., 2015; Zachariah et al., 2018). Still, behavioral comparisons between *in-situ* and *ex-situ* elephant populations have been severely limited, with a few exceptions (Rasmussen et al., 2005; Miller et al., 2016). A multi-faceted approach that supplements current efforts to enhance the physical, nutritional, and reproductive health of elephants will be necessary to address *in-situ* and *ex-situ* sustainability issues. As breeding success and conservation strategies improve, it will become necessary to better understand the behavioral plasticity of elephants in managed environments, especially in regards to intersexual behavioral differences present in the species. In particular, male elephants pose immediate and long-term challenges for wildlife managers in *in-situ* and *ex-situ* environments because of the unique condition of "musth."

Musth is a heightened sexual state in male elephants (including the African species, *Loxodonta africana* and *L. cyclotis*) that serves to announce breeding intent to females and to resolve male–male competition for access to females (Jainudeen et al., 1972a; Poole et al., 1984; Poole, 1987; LaDue et al., 2022). It occurs regularly but asynchronously among males in a population (Eisenberg et al., 1971; Poole and Moss, 1981; Poole, 1987), and the onset of musth is triggered by a surge in serum androgens (Jainudeen et al., 1972a; Hall-Martin and Walt, 1984; Cooper et al., 1990; Brown et al., 2007). These elevated androgens may cause male elephants to exhibit aggressive and/or erratic behavior (Jainudeen et al., 1972b; Poole and Moss, 1981; Hall-Martin, 1987; Ganswindt et al., 2005a), which can make musth males especially challenging to manage. As musth functions to synchronize reproduction in *in-situ* elephant populations, recognizing the value of this sexual strategy may also bolster breeding efforts to enhance the sustainability of *ex-situ* populations. Furthermore, elephant populations throughout the world managed by people within zoos and range countries (e.g., elephant camps) may require specialized care from well-experienced handlers (Hartley et al., 2019; Schreier et al., 2021), as they can be dangerous to people and other elephants with whom they interact during musth (Gore et al., 2006; Santiapillai et al., 2011). Similarly, wild male elephants can be dangerous to surrounding human communities in range countries (Sarker et al., 2015; Acharya et al., 2016; Ram et al., 2021); male elephants are disproportionately implicated in incidents of human–elephant conflict (Sukumar and Gadgil, 1988; Sitati et al., 2003; Chiyo et al., 2005; Ekanayaka et al., 2011; LaDue et al., 2021), a major threat to the well-being of local communities and the conservation of elephants alike (Williams et al., 2020; Gobush et al., 2021a; 2021b).

Contrary to the first scientific descriptions of musth that implied it

was a rather stereotyped phenomenon (Buss and Smith, 1966; Eisenberg et al., 1971), there is growing recognition that musth varies temporally, physiologically, and behaviorally (Scott and Riddle, 2003; LaDue et al., 2014, 2022), making it a dynamic state that may be influenced by various intrinsic and extrinsic factors. While we are still exploring the evolutionary and ecological processes that have shaped this variation, there are practical motivations to better understand the plasticity of musth and its consequences for adaptive management strategies, as this variation could feasibly affect breeding and wellness efforts. However, studies of musth can be logistically challenging to conduct; difficulties finding and following musth male elephants in the field may be resolved by sampling *ex-situ* populations. Even so, musth is a periodic occurrence that can be unpredictable, and there is growing consensus that musth is not a binary state (i.e., an elephant is either in musth or is not in musth). Some researchers have suggested defining multiple states (e.g., non-musth, early musth, full musth, post-musth) to describe the progression of musth (Eisenberg et al., 1971; Jainudeen et al., 1972b; Poole, 1982, 1987; Schulte and Rasmussen, 1999; Rasmussen and Wittemyer, 2002), and there are visual scales that have been developed to track this progression for African bush elephants (*L. africana*) (Poole, 1987) and Asian elephants (Scott, 2002; Finnell and Glaeser, 2016). These scales use the intensity of two visual indicators that are unique to male elephants in musth—temporal gland secretions (TGS) at the side of the head and urine dribbling (UD) on the inside of the rear legs—to gauge this progression (Fig. 1). However, systematic behavioral validation of these scales has yet to occur to assess their biological relevance.

We carried out a comprehensive investigation of male Asian elephants in an *in-situ* population in Sri Lanka and an *ex-situ* population in the United States to better understand the behavioral changes surrounding musth in these two different environments. As much as possible, we also aimed to compare results from *in-situ* and *ex-situ* populations to bring context to elephant behavior in zoo environments (Hutchins, 2006) while enjoying the more precisely controlled conditions in the *ex-situ* population. Furthermore, musth is assumed to have evolved in natural populations to enhance a male's reproductive fitness (LaDue et al., 2022) and presumably these behavioral responses would be conserved in the captive environment, and therefore we expected wild and zoo-housed elephants to exhibit similar behavioral variation around musth. The first purpose of this study was to identify intrinsic (e.g., musth status, age) and extrinsic (e.g., physical features of the environment, social access) factors that contribute to the behavioral variation of male Asian elephants around musth. We hypothesized that the behavior of male elephants would significantly vary around musth and with influences from intrinsic and extrinsic factors. The second purpose of this study was to characterize the behavior of wild and zoo-housed male Asian elephants around musth with a widely used visual scale (Scott, 2002; Finnell and Glaeser, 2016). We hypothesized that there would be distinct behavioral profiles between scores on this scale, bolstering the argument that musth is not a binary state. Support for our hypotheses would indicate any adaptive management strategy involving male elephants should consider musth as dynamic, with changing behavioral patterns as musth progresses.

2. Methods

2.1. Study sites and subjects

We observed male Asian elephants in Sri Lanka at Wasgamuwa National Park (7°43′N, 80°56′E) in the dry season between December 2018 and April 2019. Wasgamuwa is in the dry zone in the Central and North Central provinces of Sri Lanka, consists of 370.62 km² of fenced grasslands and dry evergreen forests, is surrounded primarily by agriculture, and experiences a mean ± SD daily temperature of 29.9 ± 5.6°C (during observations, mean ± SD temperature = 30.1 ± 4.1°C). Over the study period, observations took place on 57 days from a vehicle on designated roads and tracks during the park's operating hours (06:00–18:00 daily),
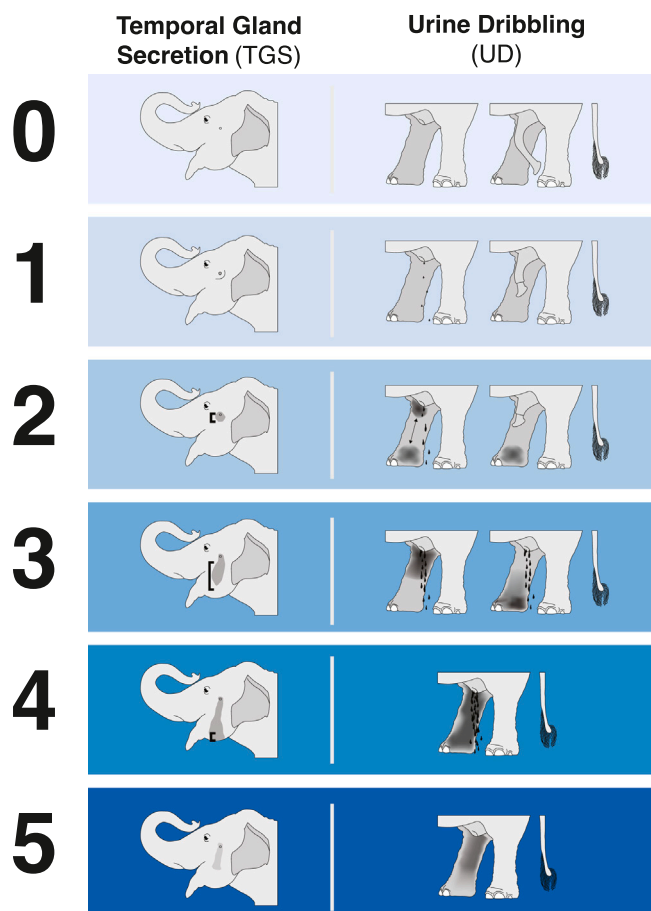
Fig. 1. Standards used to measure progression of musth in male Asian elephants, using both temporal gland secretions (TGS) and urine dribbling (UD), based on descriptions from Scott (2002) and Finnell and Glaeser (2016). Scores for each stage of TGS are: 0 = not visible; 1 = swollen temporal gland area(s), with opening potentially enlarged; 2 = gland area wet, and TGS is less than ¼ to jawline (as indicated by brackets in diagram); 3 = gland area wet, and TGS is between ¼ and ¾ to jawline (as indicated by brackets in diagram); 4 = gland area wet, and TGS is ¾ to bottom of jawline (as indicated by brackets in diagram); 5 = gland area dry, but stained with lighter color than wet TGS. Scores for each stage of UD: 0 = no visible UD, and urination occurs with penis fully extended; 1 = occasional drops of urine, and urination occurs with penis partially extended; 2 = regular dribbling and/or streams without penis fully extended, and upper or lower legs a bit stained with urine; 3 = steady streams with some dribbling from sheath, penis does not drop for urine, and upper or lower legs half-stained with urine; 4 = heavy, steady streams with wider stream than score 3, penis does not drop for urine, and legs entirely wet with urine; 5 = UD staining is dried, with lighter color than wet, and no urine dribbling. Illustrations by CAL. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

comprising 302 h of active field effort (daily average ± SD = 5.30 ± 1.09 h). Daily driving patterns alternated between three possible routes that covered all publicly accessible areas of Wasgamuwa, and we continued driving until we encountered elephants. Over the study period, we made 382 elephant sightings. Of these sightings, 256 (67.02% of all elephant sightings) included adult male elephants (those that were at least 10 years old). These male elephant sightings comprised solitary adult males (*n* = 133, 51.95% of male sightings), groups of adult males (*n* = 40, 15.63%), or mixed-sex groups containing at least one adult male (*n* = 83, 32.42%). We estimated the age class of all wild male elephants 10 years of age and older (Table S1) using modified criteria described by Varma et al. (2012). When possible, we took photographs of frontal and side views of each male elephant using a Nikon D60 DSLR camera fitted with an AF-S VR Zoom-Nikkor

70–300 mm f/4.5–5.6 G IF-ED telephoto lens (Nikon USA) to allow for future identification based on physical characteristics such as ear and tail shape, patterns of depigmentation, and the presence/arrangement of scars (Goswami et al., 2007, 2011; Vidya et al., 2014; LaDue et al., 2021). We successfully cataloged 71 male elephants over the study period, 46 of which (64.79%) were sighted multiple times. Of these 71 elephants, we successfully conducted behavioral observations on 62 (87.32%). This resulted in 151 observation sessions among wild elephants (median number of sessions per elephant = 1, ranging from 1 to 11).

We also observed 26 male Asian elephants housed at ten facilities throughout the US between July 2018 and April 2021 (mean ± SD age at the beginning of the study = 25.71 ± 15.85 years, ranging from 8.28 to 56.01 years). Six of the males in this sample were imported from the wild, and so their birthdates are estimated; all other elephants were born in human care. Routine husbandry practices at each facility (e.g., diet, feeding schedule, physical environment, social housing, training, enrichment) did not change during the study period. We aimed to sample the behavior of each male once out of musth and once while in musth (determined by the presence of temporal gland secretions and/or urine dribbling for at least five consecutive days before observations began), although logistics prevented us from collecting data from all males both in and out of musth (Table S2). This resulted in 392 observation sessions among zoo elephants (median number of sessions per elephant = 19, ranging from 5 to 30). 260 observations (66.33%) took place while the focal animal was solitary, 72 (18.37%) while the focal animal was housed only with other adult male elephants, and 60 (15.30%) while the focal animal was part of a mixed-sex group. During observations, the mean ± SD temperature was 23.2 ± 8.1 ℃.

2.2. Observation protocols

Observation protocols were approved by the IACUC at George Mason University (project number 1168839-1) and all other participating elephant facilities, and we received permission from the Department of Wildlife Conservation of Sri Lanka (permit number WL/3/2/57/18) to conduct this work. For both wild and zoo-housed elephants, we recorded musth indicators (TGS and UD scores) at the beginning of each observation session using modified versions of criteria described by Scott (2002) and Finnell and Glaeser (2016) (Fig. 1). We also noted the presence, number, sex, and age category (calf, juvenile, and adult) of any conspecifics in the area; for wild elephants in Sri Lanka, this included any other elephant visible within an estimated 100 m of the focal animal (elephants further than 100 m but still visible were presumed to be part of a separate group and were recorded as a separate sighting), and for elephants in the US, this included any other elephant in the same enclosure as the focal animal. Temperature (℃) was recorded at the beginning of observations, and for zoo elephants, we calculated the total space (in m²) where each observation took place using Google Earth Pro's polygon tool. At US facilities, we did not alter normal husbandry routines during observations— including social housing or enclosure schedules—to minimize disruption to normal behavior patterns. At all facilities, elephants were provided with food, water, and enrichment (e.g., manipulanda, feeding devices) ad libitum throughout all observations, and observations took place while keepers were absent to minimize human-directed behavior.

We observed elephants using continuous focal animal sampling for state behaviors and all-occurrence focal animal sampling for event behaviors (Altmann, 1974) using the same ethogram for both wild and zoo elephants (Table 1). We conducted all observations live using ZooMonitor (Tracks® Software and Lincoln Park Zoo) on a touchscreen tablet (Wark et al., 2019). After March 2020, we conducted most observations using video recordings (via existing closed-circuit cameras at each facility, or via a handheld camcorder operated by zoo staff) due to travel restrictions imposed by the COVID-19 pandemic. For wild elephants, each observation session lasted 15 min if possible (mean duration per

Table 1

Ethogram of state and event behaviors used during observations of male Asian elephants in the wild and at ex-situ facilities. The behaviors "locomotion" and "inactive" (marked with [†]) can occur concurrently with other state behaviors, but not with each other. Behaviors marked with [‡] occurred too rarely to be analyzed statistically.

Category	Behavior	Definition
State	Locomotion[†]	Forward or backward movement from point A to point B, > 1 body length in 3 s; includes walking and running
	Inactive[†]	Stationary space, movement < 1 body length in 3 s; includes standing, leaning, or recumbency
	Forage	Acquire, process, and/or consume food item
	Manipulate	Altering the form or position of a non-food item
	Alert	Head held high with ears erect; can occur while locomoting or stationary
	Stereotypy	Repetitive behavior with no apparent purpose; includes swaying, pacing, head bobbing, and sucking trunk
	Self-maintenance	Includes dirt bathe, water bathe, rub, or scratch
	Drink[‡]	Consume liquid
	Socialize[‡]	Engage in coordinated behavior with another elephant within 4 body lengths
	Other[‡]	Behavior not listed
	Out of view[‡]	Focal animal is not visible
Event	Chemosensory behavior	Includes olfactory behavior directed towards object of interest (i.e., sniff, check, place, flehmen), olfactory behavior directed towards an unknown source (e.g., horizontal sniff, periscope sniff), and accessory trunk behaviors (e.g., blow, flick, pinch, wriggle)
	Ear flap	Regular movement of ear(s) back and forth, more than once every 3 s; bouts are separated by at least 5 s
	Void	Urinate or defecate; does not include continuous (>1 min) urine dribbling
	Aggression[‡]	Includes behaviors such as charge (moving quickly towards object/animal/human/vehicle with head up and ears out), head shake, trunk swing, trunk throw, and tusk
	Vocalize[‡]	Audible growl, rumble, trumpet, roar, or squeak

observation $\pm$ SD = 12.73 $\pm$ 3.38 min) with a maximum of three consecutive sessions taking place on a single elephant during each sighting. If multiple adult male elephants were present during observations in Sri Lanka, the order of observation for focal animals was chosen randomly. For zoo elephants, observation sessions for each focal animal lasted 60 min, and for each site visit, we conducted sessions for each adult male once in the morning and once in the afternoon for each of five days over a seven-day timespan. If elephants were out of view for more than one-third of an observation (more than five minutes for wild elephants and more than twenty elephants for zoo elephants), the session was excluded from analysis. Likewise, any time that a zoo elephant was unexpectedly interacting with a caretaker was excluded from analysis. After this, the mean $\pm$ SD observation time per session for zoo elephants was 58.61 $\pm$ 3.30 min. All observations were conducted by the same person (CAL), and video-recorded observations were scored with > 95% agreement using an index of concordance at the beginning and end of the study period (Bateson and Martin, 2021).

2.3. Data analysis

For state behaviors during each observation session, we calculated the proportion of time the focal animal performed each behavior by summing the time engaged in each behavior and dividing by the total observable time (i.e., excluding any time that the animal was out of view or, for zoo elephants, was interacting with a caretaker). Similarly, we calculated the rate for each event behavior by summing the number of occurrences of each behavior and dividing by the total observable time, standardizing all rates to the number of behaviors per hour due to differences in the lengths of observation sessions (15 min for wild

elephants and 60 min for zoo elephants). For analyses, we only included state behaviors that occurred for greater than 2% of observation time on average, and event behaviors that occurred greater than 0.8 times per hour of observation on average; all other behaviors were excluded from analysis because they occurred too rarely to investigate statistically. After applying these exclusion criteria, we analyzed six state behaviors (locomotion, forage, manipulate, alert, stereotypy, and self-maintenance) and three event behaviors (chemosensory behavior, ear flapping, and defecation/urination). Although the behavior "inactive" met the inclusion criteria, it was mutually exclusive of any time spent locomoting, and so it was excluded to streamline the discussion of our results.

To investigate the factors that influence the patterns of these behaviors, we implemented linear mixed model (LMM) analyses using a model selection approach (Johnson and Omland, 2004; Zuur et al., 2010; Zuur and Ieno, 2016). Due to unbalanced observation counts and different environmental parameters, we constructed models for each behavior for wild and zoo elephants separately. We included the following variables as fixed effects: the interaction between musth status and age [age class in wild elephants (treated as an ordinal variable) and years in zoo elephants (treated as a numerical variable)], number of elephants present during observation, temperature (ºC), and physical space available (for zoo elephants only). To quantify musth progression (i.e., musth status), we used TGS scores only (Fig. 1); this measure has been used reliably to track progress of musth in wild and zoo settings, and TGS and UD scores were contingent upon each other (contingency coefficient, $C = 0.865$) (Table S3). We used a list of candidate models (Table S4) that we ranked via Akaike Information Criterion values (AIC$_c$, corrected for small sample sizes) via maximum likelihood estimation. We confirmed the AIC$_c$ ranking of these candidate models agreed with ranking by Akaike weight (w_i) for each behavior we analyzed. All models included the identity of the focal animal and the institution (for zoo elephants only) as random intercepts to account for repeated, unbalanced measures on the same elephants and/or the same institutions. Additionally, to account for potential temporal autocorrelation stemming from consecutive observations, we included date as a random effect in all models. We used a modified χ^2 or F test on the model with the lowest AIC$_c$ value to eliminate any non-significant variables ($P > 0.05$) until all variables in the model were statistically significant ($P < 0.05$). For the final, "best" model, we calculated marginal coefficients of determination (R^2_c) using a restricted maximum likelihood approach. Post-hoc analyses of differences in behavior between musth stages (via TGS scores) were conducted via nonparametric Kruskal-Wallis rank sums tests. As during the LMM analyses, we conducted these tests separately for wild and zoo elephants. We distinguished significant differences between musth scores via pairwise Wilcoxon rank sum tests with the Benjamini-Hochberg procedure applied to minimize Type I error (Benjamini and Hochberg, 1995). Statistical significance for all analyses was set at $\alpha = 0.05$.

We carried out all analyses and plots using R (version 4.1.0) (R Core Team, 2021). The following packages were used during analysis: *AICcmodavg* (Mazerolle, 2019), *lme4* (Bates et al., 2015), *MuMIn* (Bartón, 2019), and *tidyverse* (Wickham et al., 2019).

3. Results

3.1. Factors influencing behavioral variation around musth

We found a strong influence of intrinsic and extrinsic factors on the variation of most state (Table 2, S5, and S6) and event behaviors (Table 3, S7, and S8) we analyzed for both wild and zoo-housed male Asian elephants. Variation in time spent locomoting was best explained by the interaction between musth status and age for zoo elephants ($R^2_c = 0.635$) and musth status for wild elephants ($R^2_c = 0.595$), with locomotion generally increasing with TGS scores indicative of musth in both groups, except decreasing with age in zoo elephants. Like locomotion,

Table 2

Summary of linear mixed models (LMM) identified via model selection procedures for each state behavior for wild and zoo elephants, constructed separately. Positive estimates of fixed effects indicate positive effect of each factor on the proportion of observation time engaged in the behavior. For TGS score, TGS = 0 (non-musth) was the reference value. All other fixed effects were numeric (age measured in years, space available in m^2, temperature in °C). SE = standard error.

	WILD	Estimate	SE	*t*-value	ZOO	Estimate	SE	*t*-value
Locomotion	Intercept	0.113	0.021	5.529	Intercept	0.145	0.047	3.076
	TGS 1	0.007	0.076	0.097	TGS 1	0.171	0.079	2.167
	TGS 2	0.086	0.083	1.034	TGS 2	–0.024	0.087	–0.274
	TGS 3	0.142	0.048	2.970	TGS 3	0.429	0.041	10.344
	TGS 4	0.287	0.042	6.883	TGS 4	0.384	0.070	5.510
	TGS 5	0.041	0.112	0.361	TGS 5	0.246	0.220	1.118
					Age	–0.001	0.002	–0.577
					TGS 1: Age	–0.006	0.003	–1.928
					TGS 2: Age	0.001	0.002	0.335
					TGS 3: Age	–0.008	0.001	–5.215
					TGS 4: Age	–0.007	0.002	–3.016
					TGS 5: Age	–0.008	0.006	–1.289
Forage	Intercept	0.865	0.029	29.985	Intercept	0.686	0.091	7.524
	TGS 1	–0.165	0.121	–1.368	TGS 1	–0.879	0.126	–6.984
	TGS 2	–0.128	0.137	–0.930	TGS 2	–0.203	0.137	–1.484
	TGS 3	–0.320	0.076	–4.200	TGS 3	–0.533	0.067	–7.985
	TGS 4	–0.659	0.061	–10.875	TGS 4	–0.458	0.108	–4.251
	TGS 5	–0.115	0.178	–0.645	TGS 5	–0.483	0.355	–1.360
					Age	–0.002	0.002	–0.762
					Temperature	–0.004	0.002	–2.246
					TGS 1: Age	0.028	0.005	5.843
					TGS 2: Age	–0.005	0.004	–1.363
					TGS 3: Age	0.003	0.002	1.473
					TGS 4: Age	0.003	0.004	0.820
					TGS 5: Age	0.013	0.009	1.427
Manipulate	Intercept	0.004	0.003	1.386	Intercept	0.021	0.012	1.733
					TGS 1	0.048	0.025	1.887
					TGS 2	0.018	0.028	0.642
					TGS 3	0.104	0.013	7.787
					TGS 4	0.068	0.022	3.049
					TGS 5	0.017	0.069	0.243
					Age	–0.001	0.001	–1.019
					TGS 1: Age	–0.001	0.001	–0.993
					TGS 2: Age	< –0.001	0.001	–0.055
					TGS 3: Age	–0.002	0.001	–4.496
					TGS 4: Age	–0.001	0.001	–1.902
					TGS 5: Age	–0.001	0.002	–0.341
Alert	Intercept	0.011	0.016	0.701	Intercept	–0.009	0.012	–0.770
	TGS 1	–0.034	0.050	–0.690	TGS 1	0.135	0.029	4.637
	TGS 2	0.145	0.053	2.739	TGS 2	0.070	0.030	2.365
	TGS 3	0.208	0.031	6.689	TGS 3	0.171	0.015	11.114
	TGS 4	0.378	0.030	12.679	TGS 4	0.158	0.023	6.874
	TGS 5	0.216	0.070	3.071	TGS 5	0.133	0.076	1.738
					Age	< 0.001	< 0.001	1.151
					TGS 1: Age	–0.003	0.001	–2.761
					TGS 2: Age	–0.001	0.001	–0.998
					TGS 3: Age	–0.002	0.001	–5.260
					TGS 4: Age	–0.003	0.001	–4.263
					TGS 5: Age	–0.004	0.002	–1.778
Stereotypy	Intercept	< 0.001	< 0.001	0.985	Intercept	0.092	0.082	1.130
					TGS 1	0.121	0.107	1.125
					TGS 2	–0.056	0.119	–0.473
					TGS 3	–0.009	0.056	–0.154
					TGS 4	–0.003	0.094	–0.029
					TGS 5	0.081	0.302	0.267
					Age	–0.002	0.002	–1.037
					Space available	–2.476e–5	6.273e–6	–3.947
					Temperature	0.005	0.001	3.396
					TGS 1: Age	–0.001	0.004	–0.175
					TGS 2: Age	0.012	0.003	3.806
					TGS 3: Age	0.009	0.002	4.370
					TGS 4: Age	0.010	0.003	3.005
					TGS 5: Age	< 0.001	0.008	0.026
Self-maintenance	Intercept	0.013	0.008	1.753	Intercept	–0.017	0.008	–2.175
	TGS 1	–0.001	0.037	–0.039	TGS 1	0.019	0.008	2.287
	TGS 2	–0.005	0.044	–0.121	TGS 2	0.014	0.008	1.672
	TGS 3	0.042	0.024	1.772	TGS 3	0.018	0.005	3.583
	TGS 4	0.091	0.017	5.254	TGS 4	0.009	0.007	1.364
	TGS 5	–0.029	0.053	–0.555	TGS 5	–0.003	0.014	–0.201
					Temperature	0.002	< 0.001	5.960

Table 3

Summary of linear mixed models (LMM) identified via model selection procedures for each event behavior for wild and zoo elephants, constructed separately. Positive estimates of fixed effects indicate positive effect of each factor on the rate of the behavior (number of events per hour of observation). For TGS score, TGS = 0 (non-musth) was the reference value. All other fixed effects were numeric (age measured in years, temperature in ºC). SE = standard error.

	WILD	Estimate	SE	t-value	ZOO	Estimate	SE	t-value
Chemosensory behavior	Intercept	9.507	2.740	3.470	Intercept	39.467	6.820	5.787
	TGS 1	0.520	12.030	0.043	TGS 1	86.221	15.400	5.599
	TGS 2	8.925	13.984	0.638	TGS 2	37.814	14.581	2.593
	TGS 3	22.543	7.652	2.946	TGS 3	117.755	7.696	15.301
	TGS 4	50.903	6.110	8.332	TGS 4	129.968	10.840	11.989
	TGS 5	5.675	17.399	0.326	TGS 5	67.486	37.744	1.788
					Age	–0.155	0.160	–0.968
					Temperature	–0.633	0.201	–3.147
					TGS 1: Age	–2.025	0.565	–3.582
					TGS 2: Age	0.021	0.365	0.059
					TGS 3: Age	–1.682	0.246	–6.846
					TGS 4: Age	–2.185	0.365	–5.993
					TGS 5: Age	–1.497	1.000	–1.497
Ear flapping	Intercept	1.454	1.722	0.844	Intercept	2.725	3.931	0.693
	TGS 1	10.518	6.818	1.543	TGS 1	47.517	8.991	5.285
	TGS 2	25.737	7.619	3.378	TGS 2	14.246	5.643	2.524
	TGS 3	58.726	4.307	13.634	TGS 3	45.124	3.432	13.146
	TGS 4	60.458	3.589	16.847	TGS 4	44.812	4.275	10.482
	TGS 5	–7.018	10.065	–0.697	TGS 5	58.854	21.841	2.695
					Age	0.144	0.101	1.432
					TGS 1: Age	–1.099	0.335	–3.283
					TGS 2: Age	–0.056	0.140	–0.403
					TGS 3: Age	–0.777	0.105	–7.399
					TGS 4: Age	–0.614	0.142	–4.316
					TGS 5: Age	–1.494	0.500	–2.986
Void	Intercept	0.013	0.008	1.753	Intercept	1.155	0.086	13.360
	TGS 1	–0.001	0.037	–0.039	TGS 1	–0.280	0.206	–1.363
	TGS 2	–0.005	0.044	–0.121	TGS 2	–0.077	0.211	–0.365
	TGS 3	0.042	0.024	1.772	TGS 3	–0.360	0.127	–2.833
	TGS 4	0.091	0.017	5.254	TGS 4	–0.504	0.166	–3.027
	TGS 5	–0.029	0.053	–0.555	TGS 5	0.104	0.310	0.337

manipulative behavior followed a similar pattern of being explained by musth status and age in zoo elephants ($R_c^2 = 0.455$), but not in wild elephants. Conversely, time spent foraging decreased with musth progression; the model including only musth status best explained variation in foraging behavior in wild elephants ($R_c^2 = 0.606$), and the musth–age interaction and temperature explained foraging in zoo elephants ($R_c^2 = 0.744$). Specifically, zoo-housed elephants decreased time spent foraging as temperature increased, and older musth males foraged more than younger musth males. The time spent engaged in alert behaviors was also explained by musth status in wild elephants ($R_c^2 = 0.806$) and by the interaction of musth and age in zoo elephants ($R_c^2 = 0.728$); older zoo elephants in musth spent less time alert than young musth males. Variation in self-maintenance behavior was poorly explained by our models (zoo, $R_c^2 = 0.385$; wild, $R_c^2 = 0.197$), but our analyses suggest that musth status and temperature impact these activities in zoo elephants, and that musth status explained some variation in self-maintenance in wild elephants. Stereotypy was almost entirely absent in wild elephants, and none of the variables we included in our models explained its occurrence in that population. However, temperature, space availability, and the interaction between musth status and age were important factors in explaining stereotypy in zoo elephants ($R_c^2 = 0.662$). Variation in the frequency of chemosensory behavior was influenced by musth status in wild elephants ($R_c^2 = 0.443$) and by temperature and the interaction of musth status and age in zoo elephants ($R_c^2 = 0.860$); while increasing temperature negatively impacted rates of chemosensory behavior, the influence of age was considerably small compared to musth status. Similarly, the frequency of ear flapping bouts was also well explained by musth status alone in wild elephants ($R_c^2 = 0.824$) and by the interaction of musth and age in zoo elephants ($R_c^2 = 0.928$); again, the effect of age was less than musth status in this case. Although poorly explained by our models, the frequency with which elephants defecated or urinated was explained by musth status in the wild ($R_c^2 = 0.197$) and zoo ($R_c^2 = 0.166$) populations.

3.2. Behavioral changes associated with the progression of musth

Wild and zoo-housed elephant in our analyses exhibited similar behavioral responses as musth progressed, with clear differences in activity budgets between non-musth (TGS = 0), early and full musth (TGS = 1, 2, 3, or 4), and post-musth (TGS = 5) stages (Fig. 2a). Time spent locomoting increased when musth began and as it progressed (wild elephants: $\chi_5^2 = 42.396$, $P < 0.001$; zoo elephants: $\chi_5^2 = 85.087$, $P < 0.001$), with a steep decline during the post-musth phase to pre-musth levels (for wild elephants) or even below (for zoo elephants). Similarly, alert behavior (Fig. 2d) increased dramatically during musth (wild: $\chi_5^2 = 151.22$, $P < 0.001$; zoo: $\chi_5^2 = 151.63$, $P < 0.001$), especially during later musth stages (TGS = 3 and 4). We observed a concomitant decline in the prevalence of foraging behavior (Fig. 2b) in both groups around musth (wild: $\chi_5^2 = 76.876$, $P < 0.001$; zoo: $\chi_5^2 = 114.24$, $P < 0.001$). Elephants in both groups spent more time manipulating objects (Fig. 2c) in their environment during the later stages of musth (wild: $\chi_5^2 = 33.253$, $P < 0.001$; zoo: $\chi_5^2 = 44.142$, $P < 0.001$), but this behavior was particularly rare in wild elephants. Stereotypy (Fig. 2e) also was almost entirely absent in wild elephants (it was only observed during one observation in one elephant for approximately 20 s), and so it did not differ between musth stages ($\chi_5^2 = 44.142$, $P = 0.995$). However, it was much more common in zoo elephants; stereotypic behavior increased in duration as musth progressed ($\chi_5^2 = 105.61$, $P < 0.001$), peaking at TGS = 4. We also observed differences in self-maintenance behavior (Fig. 2f) between the stages of musth (wild: $\chi_5^2 = 27.457$, $P < 0.001$; zoo: $\chi_5^2 = 11.317$, $P = 0.045$); it was more common during the later musth stages of wild elephants and all stages of musth in zoo-housed elephants. Chemosensory behavior (wild: $\chi_5^2 = 59.728$, $P < 0.001$; zoo: $\chi_5^2 = 189.06$, $P < 0.001$) and ear-flapping (wild: $\chi_5^2 = 153.63$, $P < 0.001$; zoo: $\chi_5^2 = 175.03$, $P < 0.001$) differed significantly between musth stages in both populations, increasing dramatically during musth and peaking in later stages (TGS = 3 and 4) (Figs. 3a and
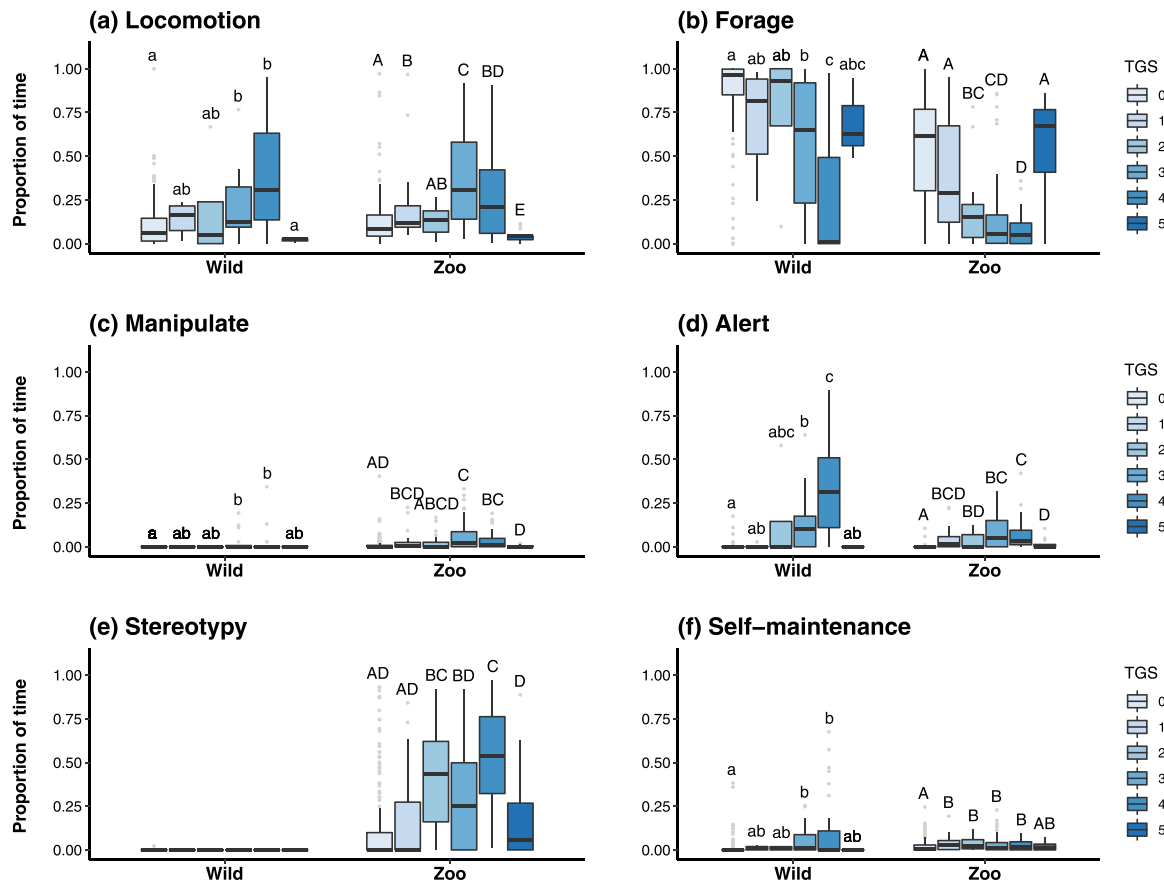
Fig. 2. Boxplots of proportion of time engaged in state behaviors at progressive musth stages (as defined by TGS scores) in wild and zoo-housed male Asian elephants. Boxes extend from the first to the third quartile, with median indicated by a thick line; fences extend to 1.5 times the interquartile range, and closed circles indicate values outside this range. Different letters above boxes indicate statistically significant differences between TGS scores ($P < 0.05$), with lowercase letters for wild elephants and uppercase letters for zoo elephants; absence of letters indicates no significant differences between TGS scores.

3b). We did not observe differences in urination/defecation rates (Fig. 3c) in wild elephants ($\chi^2_5 = 5.609$, $P = 0.346$), but these rates decreased significantly during the later stages of musth in zoo-housed elephants ($\chi^2_5 = 20.014$, $P = 0.001$).

4. Discussion

Our results emphasize the profound impact that musth has on male elephant behavior, and we observed similar behavioral responses among wild and zoo-housed elephants as the stages of musth progressed. While our results should be interpreted with caution until more *in-situ* and *ex-situ* elephant populations (and even *Loxodonta* spp. populations) can be sampled, it is striking that musth status significantly affected almost every behavior we analyzed in both populations included in this study. Additionally, we also found that in zoo-housed elephants, age interacted with musth status to predict variation in many behaviors, although this effect was minimal. In wild African savanna elephants (*L. africana*), age and musth interact to influence behavioral patterns (Poole, 1987; Taylor et al., 2020), and so it is not surprising we observed it here. However, we did not find that age influenced behavior in the wild elephants we sampled, possibly due to the somewhat non-specific age classification scheme we could use. Therefore, we suggest further studies should particularly focus on the interaction of age and musth in determining behavioral outcomes during musth in Asian elephants. Still, as we expected, foraging comprised much of the activity budgets of both elephant populations, with wild male elephants spending more time foraging (median observation time = 96.6%) during non-musth than zoo-housed elephants (median observation time = 61.4%). However, foraging time decreased precipitously with progressive stages of musth

as measured by TGS scores; the time wild elephants spent foraging during full musth (TGS = 3 or 4) decreased by approximately 66% of observation time compared to non-musth periods, and by approximately 45% during the same periods in zoo-housed elephants, despite ample food availability during all observations. As foraging time decreased around musth, time spent locomoting increased for both wild and zoo-housed elephants by about 30–40% of observation time during full musth. This behavioral trade-off is consistent with musth's evolved function: African bush elephant musth males forego foraging and adopt a roving strategy to find receptive females (Hall-Martin, 1987; Poole, 1989a; Taylor et al., 2020), and the same strategy is suspected to occur in Asian elephants (Fernando et al., 2008; Keerthipriya et al., 2020). Apparently, this motivation is conserved even in *ex-situ* environments where food and any estrous females are consistently available.

We successfully identified factors that influenced further behavioral variation in zoo-housed male elephants. For example, we found that an elephant's age interacted with musth to affect time spent locomoting and manipulating the environment, with younger elephants spending more time engaged in these active behaviors (Table 2). Other studies of zoo-housed (Wiedenmayer, 1998; Rees, 2009; Horback et al., 2014; Holdgate et al., 2016; Fazio et al., 2020) and wild elephants (Bagley, 2004; Shannon et al., 2008) have also found that younger elephants are generally more active. Zoo elephant managers that wish to enhance the physical and mental activity levels of their animals may need to provide special attention to older animals, especially as geriatric elephants may develop conditions that discourage engagement with their environments (Greene and Brenner, 2020). Physical features of the environment also affected a few of the behaviors we sampled in zoo elephants. Time spent engaged in self-maintenance behaviors such as dust-bathing and
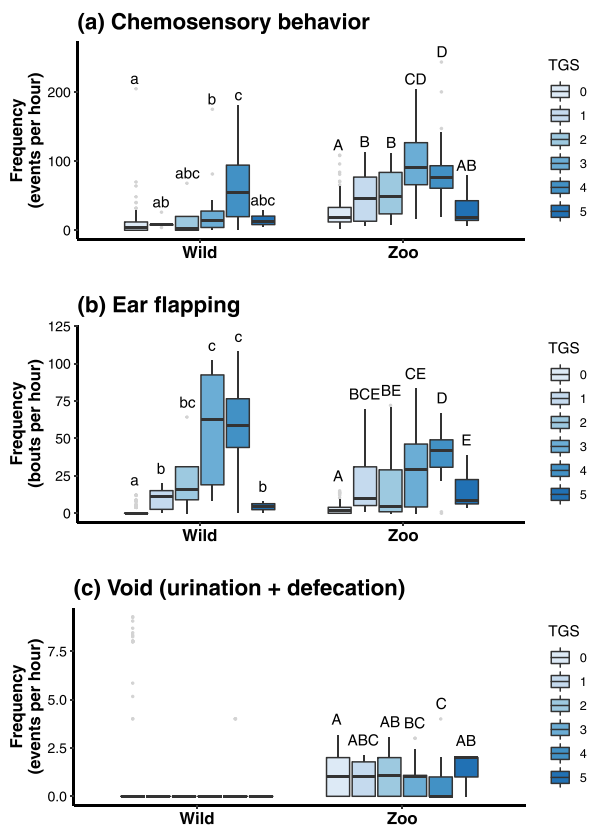
Fig. 3. Boxplots of frequency of event behaviors at progressive musth stages (as defined by TGS scores) in wild and zoo-housed male Asian elephants. Boxes extend from the first to the third quartile, with median indicated by a thick line; fences extend to 1.5 times the interquartile range, and closed circles indicate values outside this range. Different letters above boxes indicate statistically significant differences between TGS scores ($P < 0.05$), with lowercase letters for wild elephants and uppercase letters for zoo elephants; absence of letters indicates no significant differences between TGS scores.

mudding increased with higher temperatures. These behaviors aid in the ability of elephants to thermoregulate in warmer temperatures (Hiley, 1975; Weissenböck et al., 2011), and our results are supported by findings of similar behaviors in zoo-housed elephants (Rees, 2002). We also discovered environmental factors influenced stereotypic behavior: stereotypy increased slightly with higher temperatures but most notably also with decreased space availability. From a captive animal management perspective, stereotypic behavior is of interest as a potential indicator of compromised wellness in elephants and other species (Mason and Rushen, 2006). Other studies of zoo-housed elephants have found that environmental complexity rather than total space available determined behavioral diversity, activity, and/or rates of stereotypy (Holdgate et al., 2016; Meehan et al., 2016; Hacker et al., 2018; Scott and LaDue, 2019). However, these other studies focused mostly or exclusively on female elephants; as our study involved only male elephants, it provides a perspective on sexual differences in elephant behavior. Zoo-housed male elephants may be more sensitive to space constraints, as wild elephants walk longer distances to locate receptive females, especially during musth. Stereotypic behavior was virtually absent in the wild elephant population we sampled. The drive to find females appears to be conserved in *ex-situ* environments, and the inability to express these behaviors may result in stereotypy. Therefore, in addition to adding complexity to zoo environments (including opportunities to occupy areas with different temperatures), we suggest captive elephant managers offer male elephants as much space as feasible to express a range of behaviors—particularly while they are in musth.

Our findings from the *ex-situ* population may inform predictions about similar patterns that wild elephants should exhibit in different environments, as we failed to identify intrinsic or extrinsic factors besides musth status that accounted for behavioral variation among wild male Asian elephants. Some of this difficulty we encountered may a result of the homogeneity of some of the environmental variables we recorded. For example, the temperature range during our observations in Sri Lanka (mean ± SD = 30.1 ± 4.1°C, range = 4–36.5°C) was not as wide as at the zoos we visited (mean ± SD = 23.2 ± 8.1°C, range = –4.4–36.8°C). Furthermore, we could not precisely estimate wild elephant ages in the wild (Table S1), and that may have negatively impacted the model selection process. Alternatively, it is possible that musth as a reproductive strategy is less plastic in natural settings compared to zoo environments, and so some of the influence of environmental factors on behavior could be outweighed by musth status. Future efforts that investigate how the environment impacts behavioral variation around musth should sample elephants in a wider range of settings to better elucidate the influence of intrinsic and extrinsic factors. Currently, we are also undergoing an investigation of how physiological factors (e.g., hormones, body condition) may interact with behavior to result in musth variation in *in-situ* and *ex-situ* Asian elephant populations.

Surprisingly, time spent engaged in social behavior was rather low (approximately 1.8% of observation time when conspecifics were present) during our observations—even during musth. Musth presumably evolved to facilitate inter- and intrasexual interactions (LaDue et al., 2022); once thought to be largely solitary upon reaching sexual maturity, male Asian elephants are now known to have complex social lives into adulthood (Chiyo et al., 2011; Srinivasaiah et al., 2019; Keerthipriya et al., 2021). From field studies, we know that the condition of musth changes inter- and intrasexual association patterns (Poole, 1989b; Keerthipriya et al., 2020). We also expected to observe more frequent aggressive behavior during our observations of musth, as has been described in other *in-situ* (Poole, 1987, 1989a; Ganswindt et al., 2005b) and *ex-situ* (Jainudeen et al., 1972a; Lincoln and Ratnasooriya, 1996; Flora et al., 2003; Ganswindt et al., 2005a; LaDue et al., 2014; Duer et al., 2016) studies. However, these field studies have focused on aggressive behavior in *L. africana* instead of *E. maximus*, and studies on zoo-housed elephants have included human-directed aggression or have utilized reports from keepers or handlers (who are likely influenced by their personal interactions with the musth elephants) to describe aggressive behavior. There may be interspecific differences in aggression in elephants, and our analyses used observations from an unbiased observer in the absence of keepers. It is possible that once a musth male has acquired access to a female group, it would be detrimental to behave aggressively towards conspecifics; therefore aggression may simply be a result of being exposed to other stressful stimuli, such as male competitors or humans. Consequently, many studies have assigned aggression as the characteristic behavioral feature of musth. Instead, we suggest that the changes in other behaviors we have described are more appropriate. Additionally, we provide evidence that behaviors associated with communication are also characteristic of musth. There is growing evidence of the multimodality of musth as a signal, occurring simultaneously over visual, acoustic, and chemical channels (LaDue et al., 2022). Indeed, we found that chemosensory behavior increased significantly during early and full musth for zoo-housed elephants (like other active behaviors, it was also negatively associated with increasing age), and during full musth for wild elephants. Besides thermoregulation, ear-flapping may also serve a communicative function; it can act as a conspicuous visual signal (Poole, 1987), and it may waft chemical signals exuded from the temporal glands into the air. Although our models poorly characterized the variation in urination and defecation rates, these rates decreased during musth in wild and zoo-housed elephants; these matrices can carry signaling value (Rasmussen and Greenwood, 2003; Ghosal et al., 2012), but we suggest at least the decline in defecation simply resulted from decreased time spent

foraging, as has been reported in other herbivores (Smith, 1964; Rogers, 1987). Vocalizations also were exceedingly rare during the observations of the populations we studied (on average, approximately 0.23 vocalizations per hour for wild elephants and 0.52 per hour for zoo-housed elephants); a "musth rumble" has been described in a free-ranging population of *L. africana* (Poole et al., 1988; Poole, 1999), but evidence of an acoustic component to the musth signal in *E. maximus* is much more limited (de Silva, 2010). Even though these analyses did not identify changes in overall social behavior as a correlate of musth, we have shown that other behavioral changes surrounding musth almost certainly have social implications. Future studies should more carefully investigate social behavior of musth versus non-musth elephants at a finer scale to elucidate the driving factors of this unique sexual strategy.

Based on our analyses, we found that the musth scales for Asian elephants based on TGS and UD scores proposed by Scott (2002) and Finnell and Glaeser (2016) accurately tracked significant behavioral changes that occurred during musth. As these scales have not been scientifically validated with behavior, we have combined some of the consecutive TGS/UD scores with the associated behavioral changes we observed in our study to define four stages of musth that reflect ideas already present in the literature: non-musth, early musth, full musth, and post-musth (Fig. 4). We suggest that the prolonged period of non-musth (TGS = 0) is characterized by low rates of locomotion and high rates of foraging. As early musth begins (TGS = 1 or 2), locomotion and alert behavior become more common, and less foraging takes place. Full musth (TGS = 3 or 4) is defined by peak rates of locomotion and alertness, with the lowest rates of foraging. Additionally, elephants engage in frequent chemosensory behavior and ear flapping. Finally, post-musth (TGS = 5) is defined by locomotion and foraging rates

returning to non-musth, baseline levels. There appear to be intrinsic and extrinsic behaviors that contribute to individual behavioral variation during musth, and hence, these categories may not be universally applicable. Additionally, we are currently undertaking an analysis of longitudinal records of visible musth signs (i.e., TGS and UD) and various environmental variables in zoo-housed elephants to better understand the temporal variability of these proposed musth stages. Based on previous studies (Scott and Riddle, 2003; LaDue et al., 2014), we expect that male elephants will exhibit a considerable degree of variability in the duration and frequency of musth, and this may be reflected in the timing of each stage as well. Nonetheless, the behavioral profiles of each stage of musth that we identified should be studied and validated further to develop strategies for early musth detection and to track the progression of musth. In doing so, we hope to enhance the well-being of *in-situ* and *ex-situ* elephant populations, along with the safety and livelihoods of the people that live and work alongside them.

5. Conclusions

Studies like these that compare behavior between *in-situ* and *ex-situ* populations are particularly valuable because they inform management strategies across a range of conditions with the context of the evolved function of behavioral strategies in natural settings. Even in zoo environments, animals like elephants are subject to evolutionary and ecological pressures. We found that the behavioral patterns surrounding musth in Asian elephants are remarkably similar in wild and zoo-housed animals, and these behavioral changes are also likely affected by various intrinsic and extrinsic factors. Specific behaviors such as locomotion and foraging can directly impact the physical health of animals; these
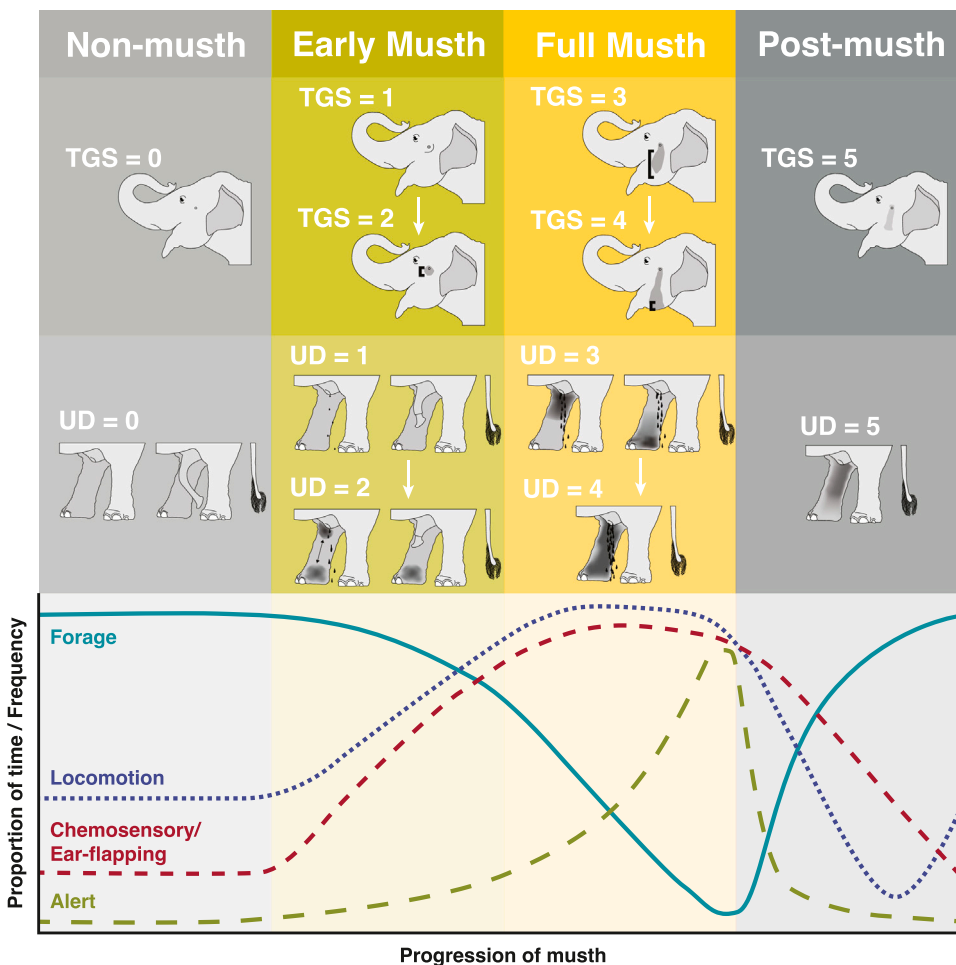

Fig. 4. Proposed behavioral stages of musth (non-musth, early musth, full musth, post-musth) in wild and zoo-housed Asian elephants based on differences in visible signs and behavior observed in wild and zoo-housed elephants. Top row: temporal gland secretion (TGS) scores. Middle row: urine dribbling (UD) scores. Bottom row: graph of generalized behavioral patterns of each stage as musth progresses (behaviors and temporal progression of musth stages are not necessarily to scale between each other). For further details on TGS and UD scores, refer to Fig. 1. Illustrations by CAL.

behaviors should be monitored to strive for optimal well-being of individual animals. Further, we found that other behaviors such as stereotypy and object manipulation also changed around musth in zoo-housed elephants. Targeted enrichment or management strategies to address these behaviors of concern may be especially important for zoo professionals to consider as their elephants progress through each musth cycle. Our study also confirmed that visible musth indicators (TGS and UD) are useful in tracking a male elephant's progression through musth, and there are behavioral changes that accurately define distinct sexual states of male elephants: non-musth, early musth, full musth, and post-musth. These visible indicators are easy to implement in a range of conditions (including *in-situ* and *ex-situ*), and we suggest that wildlife managers use them to safely and sustainably manage male elephants as we continue to learn more about musth's function(s) and plasticity. We did not find changes in overall social behavior around musth, but the identification of several behaviors related to communication that change during musth (e.g., chemosensory behavior, ear-flapping) provide ample motivation for further investigation. Musth is a unique sexual strategy that affects reproductive success in *in-situ* elephant populations, and so understanding the adaptive value and variation surrounding musth is important for the conservation of these endangered species.

CRediT authorship contribution statement

Chase A. LaDue: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Rajnish P.G. Vandercone:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Wendy K. Kiso:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Elizabeth W. Freeman:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2022.105639.

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