A Comparison of the Occurrence of Musth in the Kabini Elephant Population with Other Populations

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Abstract. We compared data (from 2009–2016) on the proportion of sightings of males in musth (versus not in musth), sex ratio, and male age structure in Nagarahole and Bandipur National Parks (Kabini population) with previously published data from Mudumalai and Kaziranga National Parks. The proportions of musth sightings were significantly lower in Kabini than in the other populations. The Kabini population had a more female-biased adult sex ratio than Kaziranga, but a similar adult sex ratio to the Mudumalai study. The male age structure was similar between Kaziranga and Kabini, whereas there was a greater proportion of very old (45+ years of age) males in Mudumalai than in Kabini. Based on the sex ratio or age structure, there were fewer old males in Kabini than in Kaziranga or Mudumalai. Thus, the occurrence or duration of musth seems to be influenced by the number of old competitors in the area.

Introduction

The Asian elephant (*Elephas maximus*) is an endangered species and occupies only about six percent of its historic range (Sukumar 2003). Humans have greatly impacted wild Asian elephant populations, through hunting for meat or ivory, and through capture for use in warfare, as a means of transport, or simply a status symbol (Sukumar 2003). Capturing wild elephants has been regulated in India (with varying success) since Asian elephants were placed under Schedule I of the Wildlife Protection Act (1972) in 1977 (amendment). However, poaching for ivory has been a serious problem. Southern India, which has the largest Asian elephant population within India and globally (Baskaran *et al*. 2011), witnessed declines in the numbers of sub-adult and adult males due to ivory poaching in the past (Menon *et al*. 1997). As only male Asian elephants carry tusks, this ivory poaching has led to skewed sex ratios, with different sex ratios in different populations (Ramakrishnan *et al*. 1998; Arivazhagan & Sukumar 2005).

Changes in sex ratio and age-sex structure can affect fecundity, relatedness, and stress (Ramakrishnan *et al*. 1998; Sukumar *et al*. 1998; Gobush *et al*. 2008). Changes in sex ratio may also affect musth, which has not been examined previously. Musth is a rut-like state of male Asian (and African savannah and forest) elephants. Males in musth show increased serum testosterone levels, temporal gland secretion, and, sometimes but not always, urine dribbling (Jainudeen *et al*. 1972a,b; Desai 1987). Male Asian elephants come into musth occasionally from the age of about ten years but the probability of coming into musth increases with age and males enter musth more regularly on an annual basis after they are over 30 years old (Daniel *et al*. 1987; Chelliah & Sukumar 2015; Keerthipriya *et al*. in press).

The ages of musth males, duration of musth, and paternity have been examined in populations of African savannah elephants with altered age structures. Older males were found to suppress younger males from coming into musth, even in poached populations with fewer old males, and were found to father the majority of offspring (Slotow *et al*. 2000, Ishengoma *et al*. 2008, Poole *et al*. 2011). Older musth males were also observed to harass younger musth males till they either left the group or stopped signalling musth

(Poole 1989). However, this might depend on the relative numbers of old and young males and the density of individuals, apart from the extent to which young males can be controlled by old males.

We wanted to compare patterns of musth in a population of Asian elephants in southern India with those of two other populations in India that had been previously studied. We compared sex ratio and male age structure in the three populations, as differences in these parameters could possibly affect the occurrence of musth. If the sex ratio was less skewed in a population, one might find a greater number of musth male sightings simply because of a greater number of males (and, therefore, male sightings) in the population. However, in that case, both musth and nonmusth male sightings would increase, leaving the proportion of male sightings in which males were in musth (calculated as the number of times identified males were sighted in musth divided by the total number of sightings of identified males) unchanged. If the age structure of the population was affected by poaching such that there were fewer old males, there were two possible outcomes. If old males came into musth more often than young males and one or a few males cannot suppress the others, there would be a greater proportion of male sightings with musth males and a greater proportion of individual males sighted in musth in the poached population. Alternatively, the remaining few old males could stay in musth for longer durations due to reduced competition from age-mates, in which case the proportion of musth male sightings of older males would increase, but the proportion of individual males sighted in musth would be low in the poached population. We also wanted to examine the effect of the presence of older males on the proportion of musth male sightings, within our study population (Kabini).

We also wanted to examine temporal variation in the occurrence of musth in our study population and compare it across other populations of Asian elephants. If there were differences in the available mating opportunities (which, in turn, could depend on seasonal differences in resource availability) across seasons, we expected the frequency of musth males and/or the age of musth males to be different across seasons. Among male African savannah elephants in Amboseli, older and more dominant males were in musth when there were more mating opportunities (wet season), while younger, medium-ranking males tended to enter musth in the dry season, possibly to avoid competition from larger musth males (Poole 1987, 1989).

Methods

Study area

We carried out our field study in the Nagarahole (11.85304°–12.26089° N,76.00075°–76.27996° E, 644 km^2) and Bandipur (11.59234°–11.94884° N, 76.20850°–76.86904° E, 874 km^2) National Parks and Tiger Reserves, southern India. Nagarahole and Bandipur lie on the two sides of the River Kabini in the Nilgiris-Eastern Ghats landscape. The habitat primarily includes dry deciduous and moist deciduous forests. Because of a dam on the River Kabini, the area around the Kabini backwaters forms a large, open, grassy habitat for elephants and other herbivores to congregate during the dry season. The Nagarahole-Bandipur population centred around the Kabini backwaters (henceforth, called the Kabini population) has a high density of about ~1–2 elephants/km^2 (AERCC 2006). Although females above ten years of age have been considered adults in the Kabini population (Nandini *et al*. 2018), only females and males at least 15 years old have been considered as adults in this paper in order to compare the same age-classes across populations.

We compared data from the Kabini population (used previously to examine the relationship between age and musth and associations in musth, Keerthipriya *et al*. in press) with data collected previously by others in Mudumalai and Kaziranga. Mudumalai Wildlife Sanctuary (when the data were collected; Mudumalai Tiger Reserve now) is also part of the Nilgiris-Eastern Ghats landscape and lies to the east of Bandipur. It has a range of vegetation types from dry thorn through deciduous forests to semi-evergreen forests. Elephant density in the park was ~1 elephant/km^2 (Daniel *et al*. 1987). Kaziranga National Park is located in northeastern India, along the floodplains of the River Brahmaputra. The habitat in the park is primarily riverine, with grassland and semievergreen forest. Elephant density was about 1.2 elephants/km^2 in 2011 (KNP Forest Department 2011).

Field data collection

We collected field data in Nagarahole and Bandipur from March 2009 – August 2016, although a large part of 2010 was not sampled due to permit issues. Sampling was carried out in a stratified manner, with greater intensity of sampling around the Kabini reservoir and decreasing intensity away from it in both directions (Nandini *et al*. 2017). We drove along pre-selected routes (Nandini *et al*. 2017) and sexed, aged, and individually identified elephants that we encountered. We identified all the males that we saw (see cumulative number of males sighted in Keerthipriya *et al*. 2018, Supplementary material). Identification was carried out based on various natural physical characteristics (Vidya *et al*. 2014).

We considered all elephants ≥15 years as adults in this study, to be consistent with the classification in the Mudumalai and Kaziranga populations. Adults were aged based on body and skull size, using semi-captive elephants of the forest department in the same area as reference (Vidya *et al*. 2014). Males from the age of 5–20 years were placed in five-year age-classes and those above 20 years old, into ten-year age-classes, and all of them were assigned a probable date of birth based on (usually) the median age of the age-class and the date of first sighting. Adult males were also grouped into two broad age-classes of 15–30 years and ≥30 years for some analyses as these age-classes were found to have different patterns of male-male associations (Keerthipriya *et al*. 2018).

Males that were at least 10 years old were assessed for their musth status and classified as being in musth if they had temporal gland secretion and/or urine dribbling, and as nonmusth if they did not have either of these (Fig. 1). For the purpose

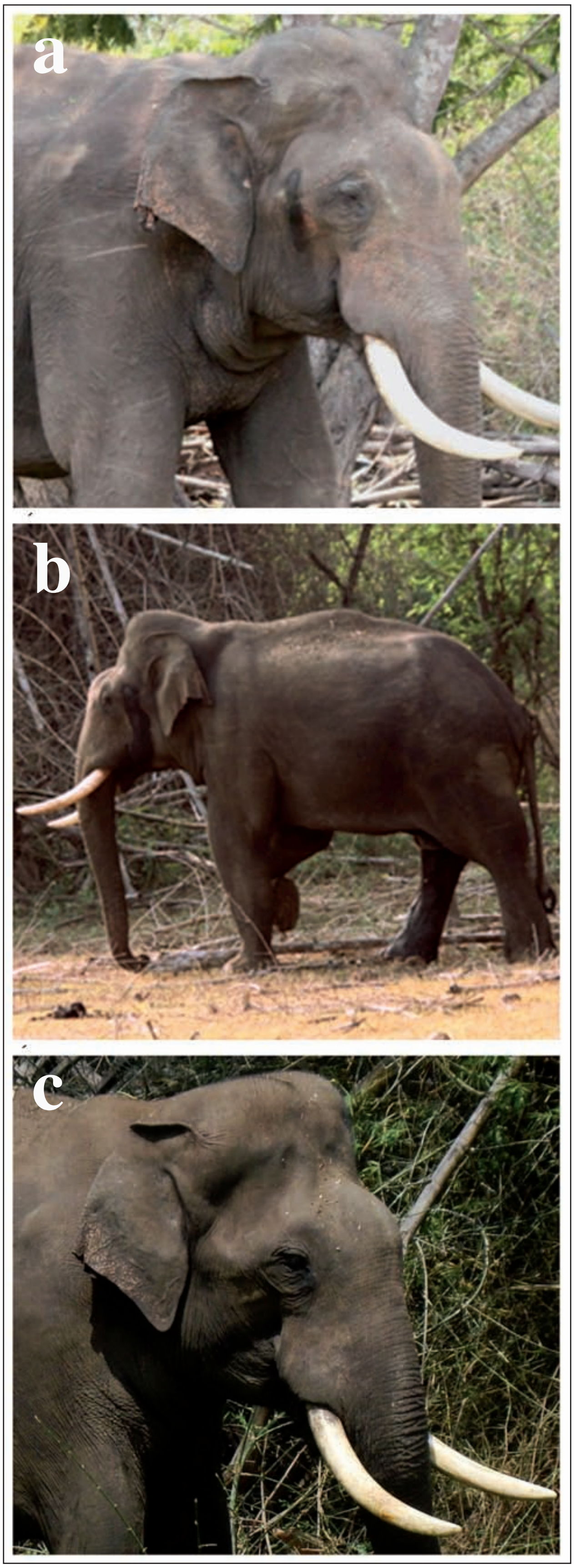

Figure 1. Male 'Horace' showing different musth statuses: a) in musth with temporal gland secretion, b) in musth with temporal gland secretion and urine dribbling (note the stained inside of the hind leg), c) not in musth.

of musth status, sightings of males were counted once a day.

Age-class-specific proportions of musth male sightings

We compared the age-class-specific proportions of musth male sightings in Kabini with those in Kaziranga based on data from Chelliah & Sukumar (2015), and with those in Mudumalai based on data from Daniel *et al*. (1987). If the age structures were different across populations, it would not be correct to directly compare the numbers of musth males of different age-classes in the different populations. Therefore, we used the age-class-specific proportions of musth male sightings (total number of musth days of males of an age-class / total number of days when males of that age-class were seen) for comparison. The proportions of musth male sightings were available for different age-classes from the Kaziranga population (Chelliah & Sukumar 2015; termed capture probability in that paper). We calculated the proportions of musth male sightings for the same age-classes from the Kabini population and compared the proportions of musth males in Kaziranga and Kabini separately for each age-class using tests for differences between two proportions in Statistica 7 (StatSoft, Inc. 2004). The percentage of sightings in which adults of different age-classes were sighted in musth in Mudumalai was provided by Daniel *et al*. (1987). Therefore, we compared those proportion values with the proportions for the same age-classes in Kabini.

Sex ratio

We calculated the sex ratio (reported as 1: number of adult females per adult male) for the study population using the number of adult males and adult females that were identified during the study period. The sex ratio was then compared to the ratios reported from Mudumalai (Desai 1987) and Kaziranga (Chelliah & Sukumar 2015). We also calculated the sex ratios for the months of January – May (reported as 1: number of identified adult females sighted in that month/ number of identified males sighted in the same month) and correlated them with the proportions of identified males who were sighted in musth in that month. This was done using a Spearman's rank-order correlation in Statistica 7 (StatSoft, Inc. 2004).

Age structure of populations

Chelliah & Sukumar (2015) had provided the number of individually identified males of various age-classes that were identified in Kaziranga. We classified our data similar to theirs (based on male age at the midpoint of the study) and compared the age structures of the two populations by performing a *G*-test of independence (Sokal & Rohlf 1981) on the numbers of identified males of various age-classes in the two populations. Data on the numbers of identified males in different age-classes were not available from Mudumalai. Instead, we obtained the number of sightings of adult males of various age-classes in Mudumalai from Daniel *et al*. (1987) and compared them with those in the same age-classes in Kabini (number of sightings in Kabini was calculated as the sum of the sightings of all individually identified males of that age-class) using a *G*-test of independence. As the number of sightings in Mudumalai was obtained from graphs in the paper (Daniel *et al*. 1987), they are approximate (but accurate within ± 2 units). We also compared the age structures of the Kabini population itself based on the numbers of sightings of males of different age-classes and the numbers of identified males of different age-classes (using a *G*-test of independence) to check whether the method changed the results.

We calculated the proportion of musth male sightings (out of all adult male sightings) for each year, for the years 2011–2016. For each of these years, we also calculated the proportion of 30+ males (all males above 30 years of age, including 40+ males), the proportion of 40+ males (all males above 40 years of age, including 45+ males), and the proportion of 45+ males, out of the total number of adult males sighted that year. We performed three Spearman's rank correlations, between the proportion of musth male sightings and the proportion of 30+ males, the proportion of 40+ males, and the proportion of 45+ males, using Statistica 7 (StatSoft, Inc. 2004).

Temporal variation in musth

We examined the occurrence of musth during the dry and wet seasons in Kabini. Dry and wet seasons were assigned based on the arrival and retreat of monsoon rainfall received in that year (Nandini *et al*. 2017). We calculated the proportion of adult males of each age-class (out of the number of identified males of that age-class that were sighted, either in or not in musth) that were seen in musth during the dry and wet seasons. We analysed the logit proportions of males in musth using a factorial ANOVA, with age-class and season as factors.

Further, since the dry season in Kabini had high densities of elephants around the backwaters and the adult sex ratio could vary across months with the movement of female groups (Gupta *et al*. 2016), we examined musth within dry seasons. We split each dry season (from 2011–2016) into five months (January – May) and performed a repeated measures ANOVA (with month as the repeated measure and year as replicate) to examine differences in the logit proportions of males in musth across months. All months (January – May) from the years 2011–2016 were sampled for more than seven days (ave ± SD: 20.433 ± 5.184).

We also compared the logit proportion of males seen in musth during the probable conception peak (probably March to June, unpublished data, Kabini Elephant Project) with that during the rest of the year (July – February; for each year from 2011–2016) using a factorial ANOVA with age-class of the male and the two sets of months (Mar – Jun, Jul – Feb) as fixed factors. ANOVAs were performed using Statistica 7 (StatSoft, Inc. 2004). We also calculated the proportion of musth sightings for the different age-classes (out of the total sightings of that age-class) in different seasons, months and for the conception peak and the rest of the year, and compared the logit transformed values as described above. The proportion of musth sightings could be high because of many males being sighted in musth (in which case, the proportion of identified males in musth would also be high) or because of a few males being sighted in musth on many days (in which case, the proportion of identified males in musth would be low).

In Mudumalai, three seasons had been considered: the 'first wet season', including the months of May, June, July and August, the 'second wet season', including the months of September, October, November and December, and the 'dry season', including the months of January, February, March and April (Desai 1987). We qualitatively compared the results of the effect of seasonality on musth from Kabini with those from Mudumalai. In Kaziranga, fieldwork had been possible only during the dry season and data were not available on seasonality of musth.

Results

We identified 118 adult males in the Kabini population during the course of the study (1248 days on which fieldwork was carried out). We sighted 48 individually identified adult males when they were in musth, on 264 days, and 100 identified males when they were not in musth, on 964 days (Table 1). During the dry season, we sighted 37 identified males in musth on 212 days, and 81 identified males not in musth on 660 days. In the wet season, we sighted 19 identified males in musth on 52 days, and 64 identified males not in musth on 304 days. It is important to note that some of the identified males were sighted both in and out of musth, while others were not. Both musth and nonmusth males (different individuals) could be sighted on the same day. There was one identified male who was sighted on one day whose musth status was unknown. The study in Mudumalai by Daniel *et al*. (1987) had been carried out from October 1985 to September 1987 and 23 adult males had been identified during the study. The study in Kaziranga (Chelliah & Sukumar 2015) had been conducted during the dry seasons of 2009–2011 (November 2008 – March 2009, November 2009 – May 2010 and November 2010 – April 2011) and 132 adult males had been identified.

Proportion of musth male sightings in different populations

The proportions of musth male sightings for the

Table 1. Number of individually identified adult males of two broad age-classes sighted during the dry and wet seasons of 2011–2016 and the percentage of those males (seen in those seasons) who were sighted in musth.

Year	Age-class [years]	# Identified males Dry season	# Identified males Wet season	% Males sighted in musth Dry season	% Males sighted in musth Wet season
2011	15–30	29	20	0	0
	30+	21	17	57.1	29.4
2012	15–30	33	19	3.0	5.3
	30+	18	13	27.8	15.4
2013	15–30	27	14	11.1	14.3
	30+	20	9	20.0	0
2014	15–30	28	15	7.1	0
	30+	17	9	35.3	22.2
2015	15–30	22	16	9.1	18.8
	30+	10	8	60.0	50.0
2016	15–30	17	9	17.6	0
	30+	10	6	40.0	33.3

15–20 year age-class was not different between Kabini and Kaziranga, while the proportions of musth male sightings in Kabini for all other age-classes were significantly smaller than those in Kaziranga (values in Kabini were significantly lower than Kaziranga for all age-classes except the 15–20 age-class; test for differences between two proportions (two sided): $P_{15\text{-}20} = 0.490$, $P_{20\text{-}30} < 0.001$, $P_{30\text{-}40} < 0.001$, $P_{40+} < 0.001$; Fig. 2a). The proportions of sightings in which males of different age-classes were sighted in musth were much lower in Kabini than in Mudumalai in all three age-classes (Fig. 2b). However, as the sample sizes were not available for Mudumalai, the values could not be statistically compared.

Sex ratio of populations

The adult sex ratio was 1 male : 3.1 females in Mudumalai (Daniel *et al*. 1987), and 1 male : 2.3 females in Kaziranga (KNP Forest Department 2011). The adult sex ratio in Kabini (from identified male and female elephants in our study) was 1 male : 3.1 females. The average (across years) sex ratio between identified males and females varied across months in Kabini; 1 male : 3.30 females in January, 1 male : 2.50 females in February, 1 male : 3.95 females in March, 1 male : 4.56 females in April, and 1 male : 4.21 females in May. The number of females per male was not significantly correlated with the proportion of males in musth across months in

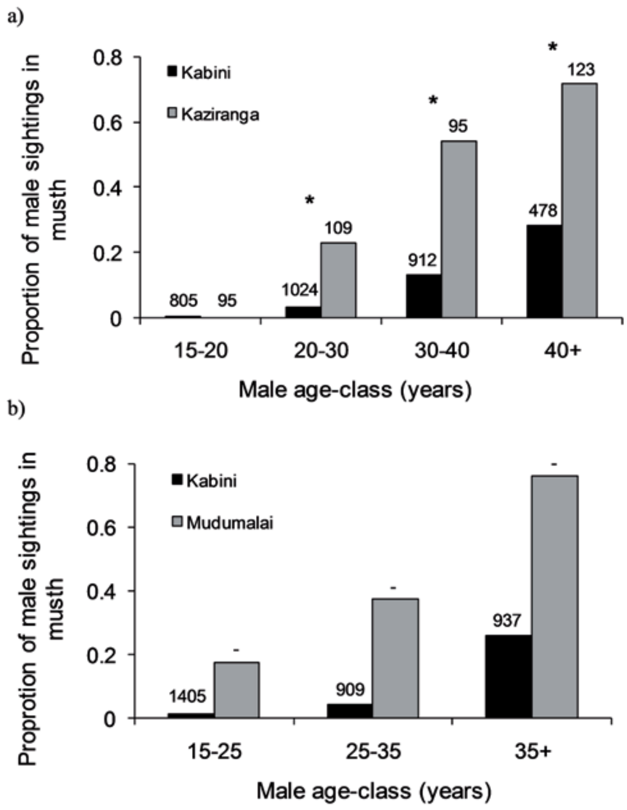

Figure 2. Comparison of proportions of sightings (of males of different age-classes) when males of different age-classes were seen in musth between a) Kabini and Kaziranga and b) Kabini and Mudumalai. Each male was recorded as having been sighted only once a day in Kabini and Mudumalai. The total numbers of sightings (not available for Mudumalai) are written above the bars.

Kabini (Spearman's rank order correlation: N = 30 months, $R = 0.194$, $R^2 = 0.037$, $P > 0.05$).

Age structure of populations

We found that the age structures (based on identified adult males) of Kaziranga and Kabini were similar (G-test of independence: $G_{corrected} = 1.658$, $df = 3$, $P = 0.646$; Fig. 3). However, age structures (based on the number of sightings of males of different age-classes) in Mudumalai and Kabini were different (G-test of independence: $G_{corrected} = 78.887$, $df = 4$, $P < 0.001$; Fig. 4). Age structures of Kabini based on the numbers of identified males and numbers of male sightings were not statistically different (G-test of independence: $G_{corrected} = 5.888$, $df = 4$, $P = 0.208$).

In Kabini, we found a negative correlation between the proportion of 30+ year old males sighted and the proportion of musth male sightings in that year (Spearman's rank-order correlation: $R = -0.771$, $R^2 = 0.594$, $P < 0.08$, Fig. 5a). However, the proportion of 40+ year old males was not significantly correlated with the proportion of musth sightings ($R = -0.314$, $R^2 = 0.099$, $P > 0.10$), and the proportion of 45+ year old males was significantly positively correlated with the proportion of musth sightings (Spearman's rank-order correlation: $R = 0.886$, $R^2 = 0.785$, $P < 0.05$, Fig. 5b). The proportion of 45+ year old males was also even more correlated with the proportion of musth sightings among 45+ year old males ($R = 0.943$, $R^2 = 0.889$, $P < 0.01$).

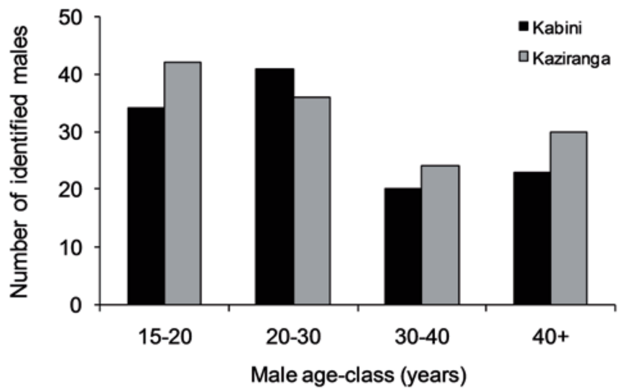

Figure 3. Age structure based on individually identified males in the Kabini and Kaziranga populations.

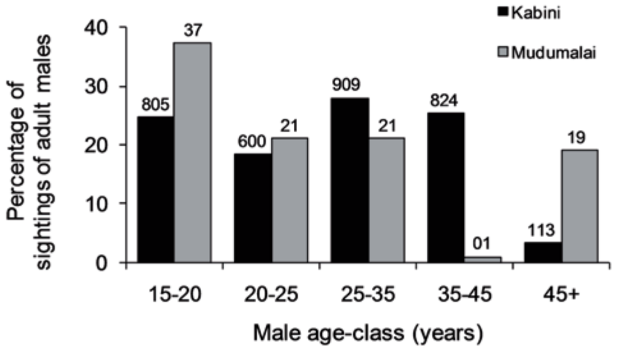

Figure 4. Percentage (out of total sightings of adult males) of sightings of adult males (not necessarily unique males) of different age-classes, in the Kabini and Mudumalai populations. The numbers of sightings are shown above the bars.

Temporal variation in musth

A factorial ANOVA on the logit proportions of males in musth (out of the identified males in that age-class) in Kabini, with age-class and season as factors showed that there was an effect of age-class ($F_{1,20} = 6.866$, $P = 0.016$), as already

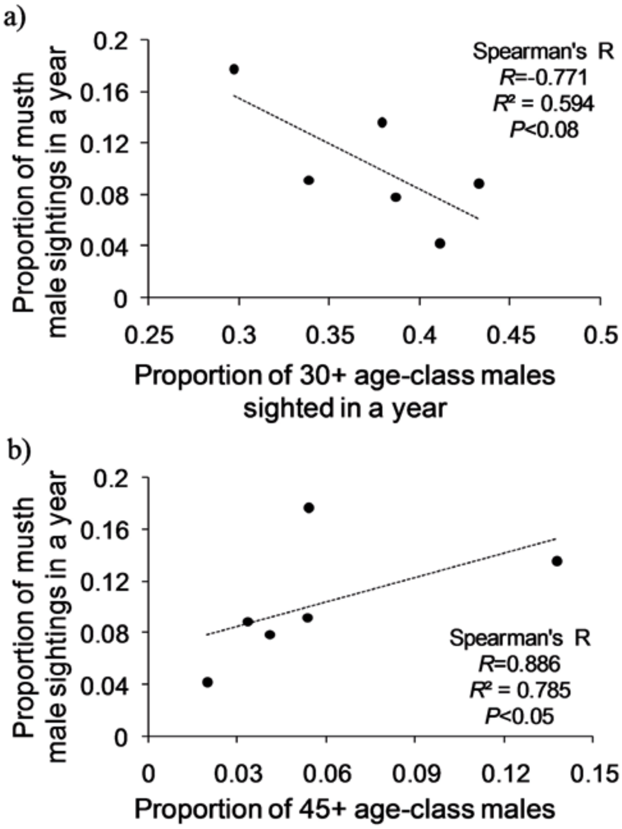

Figure 5. Correlation between a) the proportion of 30+ year old males or b) the proportion of 45+ year old males in the population in a year, and the proportion of musth male sightings in that year.

known (Keerthipriya *et al.* in press), but no effect of season ($F_{1,20}$= 2.594, P = 0.123). Thus, the proportions of males in musth were not different across seasons in the Kabini population. There was also no interaction between season and age-class ($F_{1,20}$= 0.011, P = 0.918; Fig. 6), indicating that males that came into musth during the dry and wet seasons did not significantly differ in their ages.

The repeated measures ANOVA (with month as the repeated measure, year as replicate, and age-class as the categorical factor) on the logit proportions of identified males in musth from the Kabini population showed that age-class, again, had a significant effect ($F_{1,40}$= 14.599, P = 0.003), while the interaction between months and age-class was not significant ($F_{4,40}$= 0.572, P = 0.684). Though month had a significant main effect ($F_{4,40}$= 3.470, P=0.016), none of the pairwise Tukey's HSD tests was significant (all P values >0.05, Fig. 7a). The results did not change when the ANOVA was carried out on the logit proportion of all musth male sightings (Fig. 7c).

The logit proportion of identified males seen in musth was not significantly different between the conception peak and the rest of the year (Factorial ANOVA: sets of months: $F_{1,20}$= 0.645, P = 0.431; age-class: $F_{1,20}$= 9.808, P = 0.005; interaction: $F_{1,20}$= 0.122, P = 0.730; Fig. 7b). However, the logit proportion of all musth male sightings was borderline significant/non-significant during the

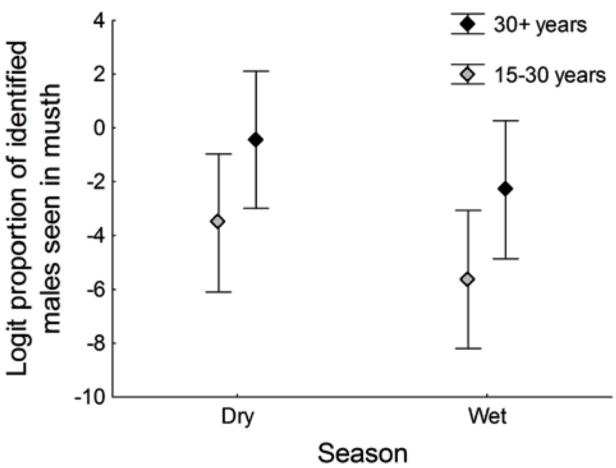

Figure 6. Logit proportion of males in musth (out of the identified males in that age-class) during the dry and wet seasons. Error bars are 95% CI.

conception peak when compared to the rest of the year ($F_{1,20}$= 4.354, P = 0.050; Fig. 7d) and age-class, again, had a significant effect ($F_{1,20}$= 19.458, P < 0.001).

Desai (1987) found that, in Mudumalai, the percentage of musth males sighted (out of the total number of males sighted) was highest in the first wet season (32.72%), followed by the second wet season (~24%, value read from graph) and was the lowest during the dry season (15.15%) and this difference was found to be significant. As already mentioned, data were collected only during the dry season in Kaziranga and hence this comparison was not possible. However, a comparison of the proportion of musth male sightings in the dry season alone between Kabini and Kaziranga also showed smaller proportions of musth male sightings in Kabini (data not shown).

Discussion

Sex ratio, age structure, and proportion of males sighted in musth

We compared the occurrence of musth, sex ratio, and male age structure between the Kabini, Kaziranga, and Mudumalai populations. We found that the proportions of male sightings in musth were significantly higher in Kaziranga and Mudumalai compared to Kabini. While males that were over 40 years old were sighted in musth in over 70% of their sightings in Kaziranga and males over 35 years old were sighted in musth in over 75% of their sightings in Mudumalai, males that were over 35 or 40 years old were sighted in musth in less than 30% of their sightings in Kabini.

Differences in the proportions of male sightings in musth may arise from differences in sex ratio, age structure, or temporal variation in musth. Kaziranga had a less skewed adult (≥15 years) sex ratio (1 male : 2.3 females from the forest department reports, values provided in Chelliah & Sukumar 2015) than in Kabini (about 1 male : 3.1 females based on identified male and female elephants from March 2009 to August 2016), but the male population age structures were similar between Kaziranga and Kabini. Although the sex ratio in subsequent years became more skewed in Mudumalai (Arivazhagan & Sukumar 2005), the adult sex ratio was similar in Mudumalai at the time of Daniel *et al*.'s (1987) study and Kabini during our study. However, the male population age structure was different between Mudumalai and Kabini, with a much higher proportion of males over 45 years old in Mudumalai compared to Kabini (although a much lower proportion of males 35–45 years old in Mudumalai).

Elephant density and season of sampling could not explain the low musth occurrence in Kabini. The densities of females in all three populations were fairly high (about or over 1 elephant/km^2) and comparable to one another. However, the local density in the restricted area of the Kabini backwaters was possibly a few times higher than the overall density in the three populations (Nandini *et al*. 2017). Therefore, if local population density were to play a role in musth occurrence, we should have found a greater, not smaller, proportion of musth males in Kabini. As there was no evidence for seasonal variation in frequency or age of musth males in Kabini, and as the proportion of musth male sightings in the dry season alone was also lower in Kabini than in Kaziranga, inconsistencies in sampling seasonality is also not an explanation for the low occurrence of musth in Kabini.

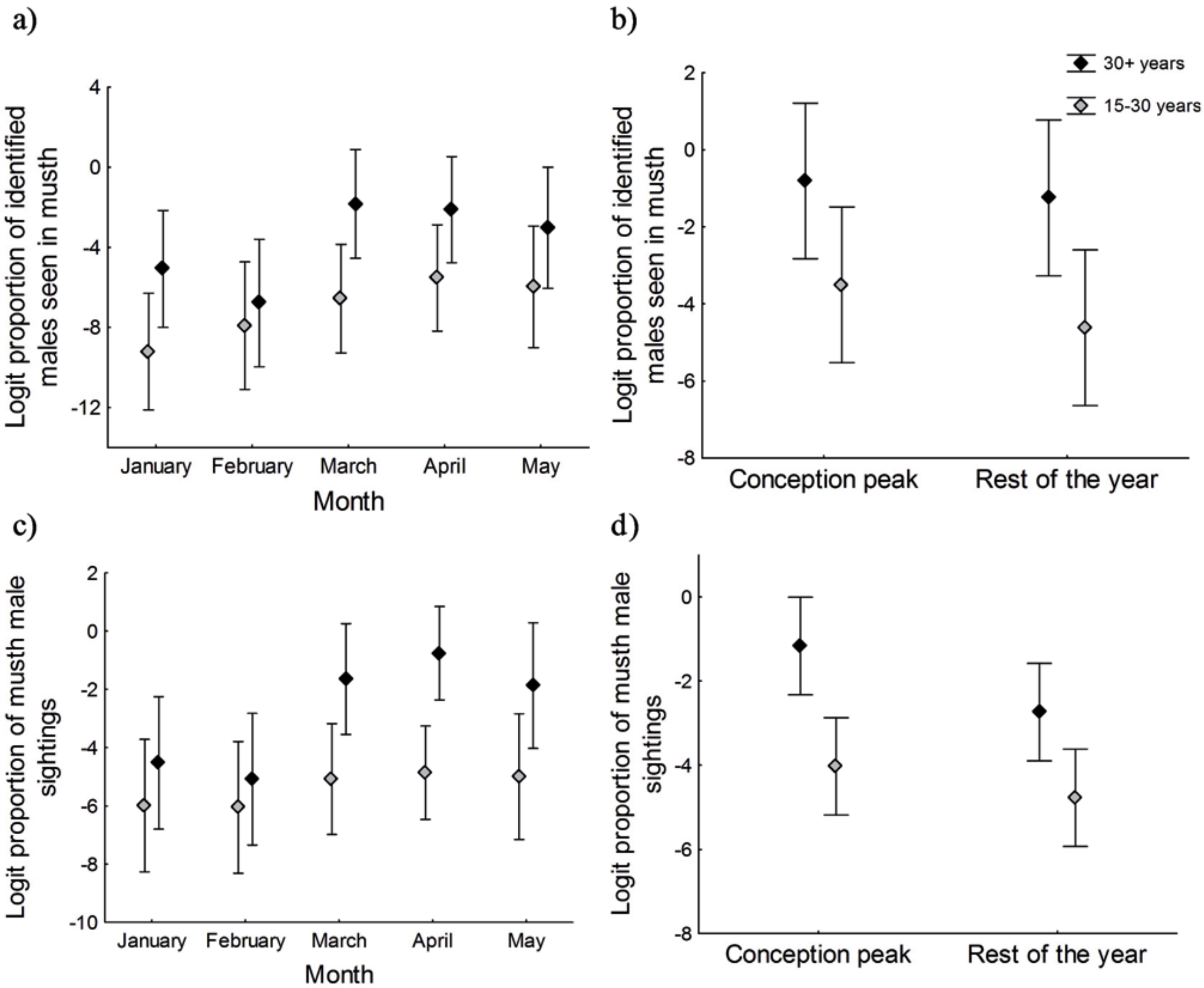

Figure 7. Logit proportion of identified males in musth of two age-classes in a) different months within the dry season and b) during the months when conceptions were probably high (Apr – Jul) and the rest of the year (Aug – Mar) and logit proportion of musth male sightings of the two age-classes of males in c) different months within the dry season and d) during the months when conceptions were probably high and the rest of the year. Error bars are 95% CI.

A less female-biased sex ratio (as seen in Kaziranga) implies a greater number of males if the population sizes are similar. There were more identified adult males in Kaziranga based on three dry seasons of sampling (132 adult males, including 30 males in the 40+ age-class; Chelliah & Sukumar 2015) than in Kabini based on sampling from 2009–2016 (118 adult males, including 23 males in the 40+ age-class). Thus, the higher number of musth sightings in Kaziranga could simply stem from more males that could enter musth. However, with the presence of more males, the total number of male sightings (regardless of musth status) will also increase and, hence, the proportion of musth male sightings (out of the total number of male sightings) should remain unchanged. Since we found that the proportion of musth male sightings (out of the total number of male sightings) was higher in Kaziranga than in Kabini, it is possible that increased competition amongst a higher number of older males in Kaziranga influences the occurrence and/or duration of musth non-linearly. This is consistent with the higher proportion of musth male sightings observed in Mudumalai, where male-male competition was possibly high because of the presence of a high proportion of males of the oldest age-class.

In the Kabini population itself, we found that years when a higher proportion of old (30+) males were seen had a lower proportion of musth sightings, while years when a higher proportion of very old (45+) males were seen had a higher proportion of musth sightings. Once again, the presence of males of the oldest age-class seemed to positively affect the overall occurrence of musth. We had expected that the presence of fewer males could either i) reduce suppression of younger males, leading to an increase in the proportion of musth male sightings (out of all male sightings) and the number of individual males in musth or ii) lead to the remaining, few older males staying in musth for longer durations, leading to a decrease in the proportion of individual males sighted in musth and an increase in the proportion of musth male sightings for older males. Our observations do not match the former expectation. They only partially match the latter expectation because the proportion of musth sightings was lower even among older males in Kabini compared to the other two populations. Instead, there seems to be a more complex effect of the presence of older males on the incidence of musth. Such a non-linear effect of competitor presence on the occurrence of musth can be tested by examining the proportions of musth male sightings in other populations with different sex ratios and different proportions of males in the old age-classes.

One trivial possibility to partially explain the results could be that there were differences in ageing animals across populations. If the ages of males in Kabini were systematically overestimated, the proportion of musth in Kabini should be similar to those of younger age-classes in Mudumalai. However, the percentage of musth sightings of 35+ year old males in Kabini (26%) was smaller than even the value for 25–35 year old males in Mudumalai (37%). As poaching is thought to have affected Mudumalai to a greater extent than Kabini (Arivazhagan & Sukumar 2005), an overestimation of ages in Kabini should have also resulted in a higher number of very old males (45+ years) in Kabini than Mudumalai, contrary to observation. Furthermore, some of the old males in Kabini had been first sighted by one of us (TNCV) during 2000–2005 and were already well-grown adult males. Therefore, consistent overestimation is unlikely. If the ages were underestimated in Kabini, it would make the proportion of males sighted in musth even smaller in Kabini than in the other populations, warranting an explanation as above.

Another possibility is that Kabini is part of the non-musth ranges of males more than Mudumalai or Kaziranga. One would require radiocollared males in all the three areas to test this. However, this is also unlikely due to the higher local density in the Kabini backwaters in summer (Nandini *et al*. 2017), which would increase the chance of finding a fertile female.

A final possibility we can think of is that possible resource limitation affects the incidence of musth in Kabini, either directly through male body condition or indirectly, through lowered female fertility due to habitat saturation. Resource limitation has been thought to affect female group sizes in Kabini (Nandini *et al*. 2017, 2018). Elephants in the Kabini population are not in very good body condition (Kabini Elephant Project, unpublished data) but this was true of Mudumalai also (in the late 1990s) from personal observations (TNCV). Although the overall densities in the three parks were similar, the relative density (relative to resources available) may be higher in Kabini with the habitat being saturated (especially, with inedible invasive species being abundant and bamboo dying out after mass flowering in early 2011). Mudumalai, at the time of Daniel *et al*.'s (1987) study did not have a saturated population because we know that it has significantly grown subsequently (Baskaran *et al*. 2010a). Habitat saturation could affect musth through the numbers of fertile females if there is female feedback on the likelihood of males coming into musth. In African savannah elephants, males have been observed to enter musth within hours of encountering an oestrus female (Poole 1989; Ganswindt *et al*. 2005). It would be interesting to see if such a feedback exists in the Kabini population, and whether a feedback in the reverse direction (from musth males to female fertility – Ajay Desai, pers. com.) exists. In the Amboseli African elephant population, the number of musth males was higher in weeks when the number of receptive females was also high (Poole *et al*. 2011), suggesting that some sort of unidirectional or bidirectional female-male feedback might exist.

Temporal variation in musth across seasons and months

Musth males in Kabini were seen throughout the year and there was no significant effect of season on the proportion of males seen in musth. This is in contrast to observation in Mudumalai National Park by Desai (1987), wherein musth males were least frequent during the dry season compared to the first and second wet seasons. It is possible that the differences between Mudumalai and Kabini in the seasonality of musth sightings might result from seasonal differences in food resources. Seasonal differences in elephant food resources have been found in Mudumalai (Sivaganesan 1991; Baskaran *et al*. 2010b) and in Kabini (Gautam *et al*. 2019), but female associations in Kabini had largely been unaffected by season (Nandini *et al*. 2017). In African savannah elephants, frequency of musth males increased with an increase in the number of oestrous females/conceptions (Hall-Martin 1987; Poole *et al*. 2011) and older, high-ranking males were seen in musth more frequently than younger, lower-ranked males during the time when there were more conceptions (Poole 1989). The timing of musth of individual males was thought to be a balance between high male-male competition during peak conception times and low availability of receptive females during other times of the year (Poole 1987; Poole *et al*. 2011). The lack of a clear peak in the occurrence of musth in Kabini is, perhaps, due to a possible lack of distinct breeding season in Kabini, although this needs to be further examined.

To conclude, we find that the proportion of musth sightings was significantly lower in Kabini than in the other populations examined and propose that this relates to the lower number of males of the oldest age-class in Kabini than in the other populations, which in turn probably ensued from differences in sex ratio (in the case of Kaziranga) or age structure (in the case of Mudumalai; which itself, could have arisen due to poaching). Resource limitation and patterns of resource distribution might also play a role, and data from other long-term studies would be useful in examining the various hypotheses we propose about the occurrence of musth.

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