

Abundance and social organization of male Asian elephants (*Elephas maximus*) in Rajaji Tiger Reserve

by

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Under the supervision of

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**भारतीय वन्यजीव संस्थान
Wildlife Institute of India**



June 2024

DECLARATION

I hereby declare that the work conducted under the thesis entitled “**Abundance and social organization of male Asian elephants (*Elephas maximus*) in Tiger Reserve**”, is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master’s in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Bivash Pandav, Scientist-G**, co-supervision of **Dr. N Lakshminarayanan, Project Scientist (Elephant Cell)** and **Dr. Samrat Mondol, Scientist-F** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.



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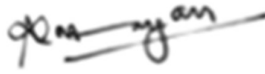
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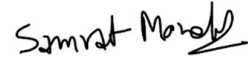
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CERTIFICATE

This is to certify that the thesis by **Abhimanyu Madhusudanan** entitled “**Abundance and social organization of male Asian elephants (*Elephas maximus*) in Rajaji Tiger Reserve**” is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Abhimanyu Madhusudanan has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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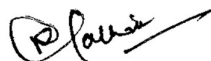
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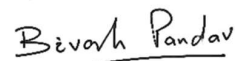
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List of Abbreviations

SECR	Spatially explicit capture-recapture
AMG	All-male group
RNP	Rajaji National Park
HFD	Haridwar Forest Division
SA	Sub-adult
EA	Early adult
YA	Young adult
PA	Prime adult
OA	Old adult
SAM	Sub-adult male
BCS	Body condition score
AIC	Akaike Information Criterion

Executive Summary

1. Asian Elephants are complex, social, and polygynous mammals living in fission-fusion societies. Male elephants are known to alternate between leading solitary lives, in all-male groups or associating with mixed-sex herds. All-male groups allow younger males to learn from older males, test strengths and spar with their peers. While much work has been done on female Asian elephant societies, studies focused on male association patterns are limited, but gaining importance in the light of human-elephant conflicts. In this study, I estimated the abundance of adult male elephants in a stretch of forest spanning over 40 km along the east bank of the river Ganga in Uttarakhand using a polygon search-based spatially explicit capture-recapture (SECR) framework. I also investigated the factors that affect male associations with different group types (All-male groups (AMG), Mixed-sex herds or Solitary) by answering the following questions: a) How are association patterns of males related to age? b) Does the frequency of association of males differ between group types? c) Are there any habitat-association relationships, and d) Do physiological and physical conditions play a role in determining the association pattern?

2. I invested a survey effort of ~3014 km to estimate the abundance of the adult male segment of the population using a capture-recapture framework. Using a combination of morphological features, I identified 34 adult males from 124 elephant sightings. Association patterns of the male elephants, following behavioural sampling approaches were also recorded during the surveys.

3. Adult male elephant density was 0.05 (SE=0.01)/km², and a derived abundance of 40 (SE=1.4) for the 475 km² study area. This demonstrates that polygon search-based SECR is an effective approach in estimating elephant abundance.

4. My results indicate a significant difference in the frequency of association of males with different group types. It also revealed that younger males are more likely to associate with a herd than an all-male group. Additionally, I found clear habitat-association relationships, with males being highly likely to form all-male groups in open habitats like grasslands and scrubs and near human habitations. While providing interesting results, the study also raises new questions on how male Asian elephant societies function, particularly within all-male groups, which warrants a long-term dedicated study and additional behavioural observations.

1. INTRODUCTION

The key tenet of any society is the inclination to form groups (Chakrabarti, 2018). The decisions animals make are between alternative courses of action in terms of their costs and benefits (Krebs & Davies, 1987). Group living has evolved because the benefits outweigh the costs. Mammalian social systems are complex and in order to understand how they develop, we must look into how the interplay of species specific characteristics and environmental factors shape social structures (Crook et al., 1976). Group living and cooperation are terms that are often used together to explain the evolution of social systems. Cooperation provides benefits even if there is an initial individual cost. It can affect the resolution of disputes within social groups and help balance out innate differences in dominance potential between individuals in group-living species (Smith et al., 2023). Evolutionary strategies like group living exhibit a range of alternatives between and within species (Krebs & Davies, 1987). This intraspecific variation in social structure is found in a range of mammalian species (Connor et al., 2017) and owing to divergent strategies of male dispersal and female philopatry in polygynous species, the sexes are usually segregated (Greenwood, 1980; Keerthipriya et al., 2021; Kie & Bowyer, 1999; Shannon et al., 2008). These sex-based differences may increase the propensity to form kin-based intragroup associations, making them more common in females than males (Smith et al., 2023). The intensity of intrasexual competition further diminishes the propensity of males to form cooperative associations, making these associations particularly rare among mammals (Clutton-Brock, 2009; Patzelt et al., 2014; Van Hooff & Van Schaik, 1994). This sets the stage for conflict and not cooperation.

Even so, male associations have been reported across species. The reasons for this can have different proximate and ultimate causes in different species, and they often prove difficult

to determine (Caro, 1998). In several primates, such as the Guinea baboons *Papio papio* (Patzelt et al., 2014), there is extensive cooperation among males that are often unrelated and in Chimpanzees, *Pan troglodytes* (Langergraber et al., 2007; Nishida & Hosaka, 1996), where they form hunting patrols. Male bottlenose dolphins (*Tursiops* sp.) are also known to form coalitions to defend oestrous females to increase their reproductive success (Connor et al., 1992; Randić et al., 2012; Wiszniewski et al., 2012), and joint foraging by coastal river otters have also been reported (Blundell et al., 2004). Some felids also form cooperative male alliances, such as joint dispersal in male cheetahs (*Acinonyx jubatus*) (Caro & Collins, 1987). Most of these associated males tend to be kin. Therefore, it can be understood that male alliances often form for protection, access to mates, improved hunting abilities, and learning social behaviours - all of which can increase individual survival and reproductive success over time. But there are certain species in which kinship is not the reason for association among males or females (Silk, 1994). For example in species with female dispersal like bonobos (*Pan paniscus*), where female associations are seen more often than in males (Nishida & Hiraiwa-Hasegawa, 1986; Silk, 1994), and in sperm whales (*Physeter macrocephalus*) in which unrelated males form long-term associations lasting for over two years (Kobayashi et al., 2020). Coalitions or alliances may therefore also form for reasons other than kin-selection.

Access to resources by coalitions necessitates resource-sharing. Therefore, coalitions or alliances only become optimal when the benefits of associating with other males, who are helpers as well as competitors, outweigh the cost of resource-sharing (Chakrabarti, 2018). The formation of such male alliances or coalitions can thus be explained by mutualism and reciprocity (Clutton-Brock, 2002).

In elephants, which have complex social organization in the form of fission fusion societies with strong social bonds and exhibit pronounced sexual dimorphism, male alliances appear common. There is also a strong selection pressure on males for larger body size

(Douglas-Hamilton, 1972; Fishlock & Lee, 2013; Moss & Poole, 1983; Sukumar, 2003). Complex pathways of alliance formation often require a species to be long-lived and have high cognitive ability (Chakrabarti & Jhala, 2017; Olson & Blumstein, 2009; Ridley et al., 2005). Both of these are characteristics associated with elephants. Social learning and the cultural transmission of knowledge were found to be some of the drivers for younger bulls to associate with older ones in African elephants (Chiyo et al., 2012). The study of these association patterns can help us understand how individual characteristics like age can influence social structure which may shed light on several aspects of behavioural ecology like the evolution of social life-history (Machanda & Rosati, 2020; Weiss et al., 2021). The drivers of such associations may also vary across landscapes and are context-specific, as elephants are known to respond to local ecological and anthropogenic stressors (Srinivasaiah et al., 2021). This also has relevance to understanding drivers of human-elephant conflict, such as association patterns during crop raiding.

There also could be an effect of density and abundance on the inherent social structure in the region. Higher abundance could mean increased encounters between individuals, fostering social interaction. Low abundance of males can reduce the opportunities for interaction and cause males to either be solitary or only form loose associations. These social relationships therefore depend on the frequency of encounter which in turn is related to elephant density and abundance (Sukumar, 2003). Several direct sighting and indirect methods have been used to estimate elephant numbers in India (reviewed in Vijayakrishnan et al., 2020). But with individual identification using morphological features possible for adult male elephant, capture-recapture methods provide an alternative with spatially explicit capture-recapture being a reliable method to estimate elephant densities and abundance (Goswami et al., 2019).

With this study, I investigated the association patterns of male elephants and the factors affecting these associations. I also estimated the adult male elephant abundance using a spatially explicit capture-recapture framework to establish whether ecological constraints on male availability could influence the observed patterns of association.

1.1 Objectives

1. To estimate the abundance of adult males

a. What is the abundance of adult males in the study area?

From the context of this study, it is important to know the abundance as it can influence the association pattern of males. Small populations may only allow males to be solitary or form loose associations. A large population will enable males to be more selective.

b. What is the age structure of male elephants?

c. What is the adult sex ratio?

-

2. To understand factors influencing male association patterns

a. What is the relative frequency of different social organization in males?

b. How do association patterns vary with age?

c. Do physiological conditions like musth affect association patterns?

d. Is there any difference in the body condition of males associating with different group types?

Hypothesis 1: Male elephants in better body condition are more likely to form or join all-male groups compared to those in poorer body condition.

Males with good body condition will exhibit a higher propensity to compete for access to resources and will be perceived as more desirable group members within all-male associations.

Hypothesis 2: Body condition is positively correlated with the frequency of interactions within mixed-sex groups, with males in better body condition being more actively involved in social interactions within these groups.

Males with better body condition may have higher energy reserves for interactions, potentially influencing their preference for this association pattern.

e. Do association types vary from one habitat type to the other?

No prior expectation

1.2 Association patterns of male elephants

Female Asian elephant societies are now understood to be slightly different from those of African elephants (De Silva, Ranjeewa, & Kryazhimskiy, 2011; Nandini et al., 2018) though both matriarchal societies, with them and their dependent offspring living together in a group, males dispersing from their natal groups and being largely solitary thereafter (Douglas-Hamilton, 1972; Moss & Poole, 1983; Nandini et al., 2018; Sukumar, 1989; Vidya & Sukumar, 2005). In most non-monogamous species, males are the ones to disperse from their natal groups (Greenwood, 1980; Silk, 1994). Inbreeding avoidance is thought to be the main function of such dispersal (Caro, 1998). Dispersal also profoundly alters the social environment in which subsequent behavioural development occurs (Smale et al., 1997).

Male elephant associations and social structure are well-studied in African elephants (*Loxodonta africana*) (Lee et al., 2011; Moss & Poole, 1983). They alternate between solitary lives to living in all-male groups or associating with mixed-sex herds with both males and females (Chiyo et al., 2011). The timing and process by which young male elephants separate from their family units are influenced by a combination of factors, including the dominance status of their mother, the presence of other male elephants to provide social interaction and their physical development (Lee et al., 2011). Social structure within all-male groups is also important as a stable hierarchy benefits younger bulls and helps establish strong bonds (Murphy et al., 2019; O'Connell-Rodwell et al., 2011). All-male groups in African elephants allow individuals to test their strengths, spar with their peers, and enable younger males to learn from older males (Chiyo et al., 2011, 2012; Keerthipriya et al., 2021). Chiyo et al. (2011) showed that males associate in large groups of related individuals of similar age, proving the role of kin selection within all-male groups. However, these all-male groups have been associated with

an increased propensity to raid crops for both African and Asian elephants (Chiyo et al., 2012; Srinivasaiah et al., 2019; Sukumar & Gadgil, 1988).

While much work on association patterns of male African elephants has been done (Chiyo et al., 2011, 2012; Goldenberg et al., 2014; Morris-Drake & Mumby, 2018; Moss & Poole, 1983; O'Connell, 2020; Shannon et al., 2008), studies on Asian elephants are few (Keerthipriya et al., 2021; LaDue et al., 2022; Srinivasaiah et al., 2019). All-male groups in Asian elephants have been noted earlier in India (Keerthipriya et al., 2021; Srinivasaiah et al., 2012; Sukumar, 2003; Sukumar & Gadgil, 1988) but have only been recently reported to be a novel behavioural strategy in human-dominated landscapes (Srinivasaiah et al., 2019). Sukumar (2003) reported the occurrence of all-male groups along the banks of Kabini reservoir in Nagarhole National Park with the largest group size of 8, but he also describes them as being “loosely spaced congregations”. Recent studies on all-male groups in Kabini have shown that Asian elephant males spent the least proportion of time in all-male groups (Keerthipriya et al., 2021) as compared to African elephants, where the trend was reversed (Chiyo et al., 2011). Keerthipriya et al. (2021) also showed that older males preferred to associate more with older peers than younger males, pointing to the fact that older males associated with each other to test strengths. One study from Sri Lanka looked at how age and musth affected association patterns and found that non-musth males with increasing age associated more with all-male groups (LaDue et al., 2022). The tendency of individual elephants to selectively choose whether to associate in temporary or stable same-sex groups, mixed-sex groups or remain solitary may represent an important facet of their life history adaptations (Srinivasaiah et al., 2012). This could also be an artefact of the population size of males.

1.3 Population estimation methods for elephants

Estimating the population size of Asian elephants has been difficult due to the dense habitats they primarily inhabit (De Silva, Ranjeewa, & Weerakoon, 2011). Several direct and indirect methods have been used for population estimation in India. Direct sighting methods like visual detections along a line transect to estimate population density under a distance sampling framework have been reliable (Jathanna et al., 2015). Other censusing methods like block counts, waterhole counts and simultaneous counts are also used but are labour-intensive and therefore, other indirect methods like dung counts are more commonly used (Vijayakrishnan et al., 2020). DNA-based capture-recapture methods for Asian elephants have been shown to generate reliable estimates of population size (Chakraborty et al., 2014) but given its logistic limitations, it is not a widely used technique. Mark-resight methods have also been used for both African (Morley & Van Aarde, 2007) and Asian elephants (Williams, 2002). Most capture-recapture studies are inherently spatial in nature, with capture probabilities depending on the location of traps relative to animals (Borchers, 2012; Gogoi, 2015). Goswami et al. (2007) showed that capture-recapture methods can be used for reliable abundance estimation of adult male elephants, where individual identification is possible. Building on such studies, spatially explicit capture-recapture (SECR) models have also emerged as an appropriate, appealing and robust method for assessing populations of these wide-ranging species (Goswami et al., 2019). While different types of detectors, such as proximity and count detectors, are conventionally used for SECR, polygon or transect detectors are now also being used (Efford, 2023). Labour-intensive methods like polygon search have not been implemented in assessing Asian elephant numbers across their range of occurrence.

2. METHODS

2.1 Study area:

The study was conducted in the eastern part of Rajaji National Park (RNP) and the adjoining ranges of Haridwar Forest Division (HFD). The Rajaji National Park (29° 51' N to 30° 15' N, 77° 52' E to 78° 22' E) and the Haridwar forest division (29° 58' 6.02' ' N, 78° 13' 9.82' ' E) are located in Uttarakhand and fall under the Gangetic plains biogeographic zone (Rodgers & Panwar, 1988). The study area comprises the Chilla and Gohri ranges of RNP and three HFD ranges, namely, Shyampur, Rasiabad and Chiriyapur, totalling around 475 sq. km. The altitude ranges between 300-1000 m asl. The area receives most rainfall between mid-June and September, followed by the arrival of winter from November through February and the dry season between March and May (Nigam et al., 2022). November is the driest month with just 4mm of rain. Highest precipitation is seen in July, with an average of 375 mm (Nigam et al., 2022).

The principal vegetation in the region includes tropical dry and moist deciduous forests, scrub vegetation, alluvial grasslands and forest plantations dominated by *Tectona grandis* and *Eucalyptus* spp. (Johnsingh et al., 2004; Nigam et al., 2022). The Vegetation communities include Sal (*Shorea robusta*) dominated forests along, Sal-mixed forests of *Shorea robusta*, *Mallotus philippensis* & *Lagerstroemia parviflora*, riverine forests of *Acacia catechu*, *Dalbergia sisoo* & *Syzygium cumini* and mixed forests of *Lagerstroemia parviflora*, *Holoptelea integrifolia*, *Ehretia laevis*, *Adina cordifolia* & *Anogeissus latifolia* (Johnsingh et al., 2004; Nigam et al., 2022; Williams, 2002).

The region is part of a corridor connecting Rajaji to Corbett Tiger Reserve through the Lansdowne Forest Division. While supporting a sizeable population of Asian elephants (*Elephas maximus*), the region is also home to a wide range of fauna, including tiger (*Panthera*

tigris), sambar (*Rusa unicolor*), chital (*Axis axis*), nilgai (*Boselaphus tragocamelus*), wild pig (*Sus scrofa*), leopard (*Panthera pardus*), striped hyena (*Hyaena hyaena*), Swamp deer (*Rucervus duvaucelii duvaucelii*) and other mammalian as well as a wide range of herpetofauna and avifauna.

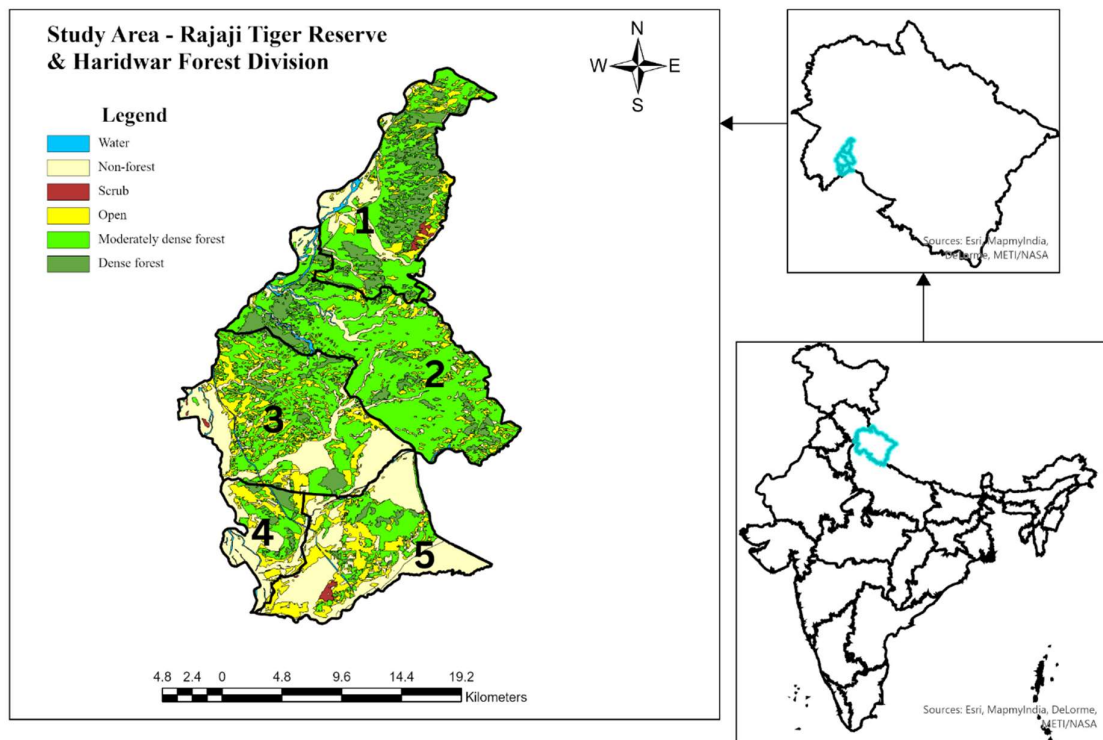


Fig 1 : Map showing the study area: 1. Gohri and 2. Chilla ranges of Rajaji National Park & 3. Shyampur, 4. Rasiabad and 5. Chiryapur Ranges of Haridwar Forest Division, ca. 475 km² along the east bank of river Ganga.

2.2 Field methods:

2.2.1 Abundance estimation

In order to avoid spatial “holes” and distribute the sampling effort systematically, I divided the entire study area of 475 km² into sampling grids of 25 km² (n=19). Each grid was visited on ten separate occasions between February 2024 and May 2024. Every visit to a grid was defined as an occasion. Searches for elephants were conducted both on foot and in a four-wheeler. I, along with a team of three field assistants, conducted searches for elephants both during morning and evening till sundown. We followed trails usually used by forest department field staff to look for elephant signs during the morning and then further tracked elephants on foot wherever signs of recent use were seen, including dung, tracks, and breaking of branches and foliage. All the tracks were recorded using the Locus Map mobile app.

The polygon search method is an extension of the SECR, wherein the detectors are “active” compared to passive detectors like stationary camera traps. (Gogoi et al., 2020). Once an adult male elephant was spotted, the location was recorded using the Locus Map mobile app.

Individual identification of males was done based on fixed morphological characteristics. (Goswami et al., 2012). The traits that were considered are given in Table 1. Other variable features, such as injuries, scars, ear holes, tail length, presence or absence of tail bush, and warts, were also considered wherever applicable.

For each adult male encountered, I attempted to take (i) front-on pictures with the head down when the animal was not alarmed to have a clear view of tusk and ear morphology; (ii) side profiles to ascertain tusk angle and tail length, and also to identify scars and warts on the body; (iii) a clear side or frontal picture of both ears (Goswami et al., 2007). All pictures were taken using a Nikon P9500 point-and-shoot camera.

A unique ID was created for each individual identified, and the capture history was generated accordingly.

Tusk	Presence/Absence Length Arrangement Thickness
Ear	Fold Lobe

Table 1 : Details of morphological features used for identification of individual bull elephants

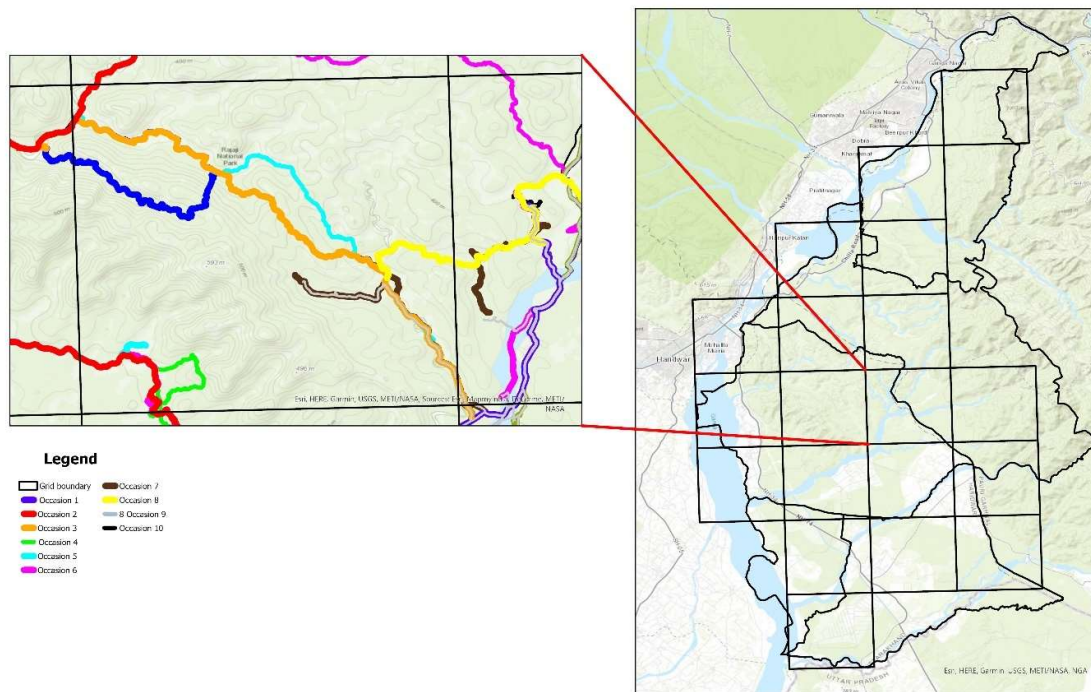


Fig 2: Map of the study area showing sampling grids of 25 km² each (n = 19) and the trails in which search efforts were carried out.



AM007, 06/05/2024
29.94953° N, 78.22592° E



AM007, 15/04/2024
29.88987° N, 78.30345° E

Fig 3 : Example of a photographic recapture of an adult male. Individual ID, date and location are given for each occasion the bull was captured

2.2.2 Association patterns

Data on association patterns was collected concurrently with the surveys for abundance estimation. Males were classified into one of the three group types- all-male group, mixed-sex herd or solitary based on their association. Mixed-sex herd group composition and size were also recorded whenever they were encountered. All individuals, both males and females were classified into the age categories as shown in Table 2. The adult age classification was used only for males.

This age classification was a modification of Fernando et al., 2022 and Natarajan et al., 2023. The adult age classification was followed only for males. It is also important to note that beyond 20–25 years of age, the shoulder height of adult elephants is known to asymptote. Therefore for these animals, other morphological traits such as degree of folding and depigmentation of the ears, temporal and buccal cavity depression, and prominence of domes were also assessed to place them in the appropriate age classes (Natarajan et al., 2023; Srinivasaiah et al., 2019; Sukumar, 1989).

<u>Age- class</u>	<u>Term</u>
<1 year	Calf/Infant
1-3 years old	Juvenile I
3-6 years old	Juvenile II
6-10 years old	Juvenile III
10-15 years old	Sub-adult
15-20 years old	Early adult (EA)
21-30 years old	Young adult (YA)
31-50 years old	Prime adult (PA)
>50 years old	Old adult (OA)

Table 2: Age classification for elephants as adopted from Fernando et al. (2022) and Natarajan et al. (2023)

Data on the four factors of interest were collected when elephants were encountered. While each individual was assigned to an age-sex category, each sighting was assigned a habitat type – dense forest, moderately dense forest, open forest, scrub, grassland or non-forest. Data on males' physiological condition- musth and non-musth, was also collected. Males in musth were identified based on different stages of secretion of musth fluid from the temporal glands and urine dribbling. I followed Fernando et al. (2009) in assessing the body condition of males based on the relative scoring of body characters. The scores ranged from 1 (poor) to 10 (healthy condition). Body condition scores were assigned to individual males using photos and videos.

2.3 Analytical methods

2.3.1 Abundance estimation

Abundance was derived from the density estimated using maximum likelihood-based polygon search spatially explicit capture-recapture (Efford, 2011, 2023; Gogoi et al., 2020), which accounts for the spatial distribution of elephants. Essentially, it calculates two parameters: σ , the spatial detection function's scale parameter, which indicates the rate at which the probability of finding an animal decreases as the distance from the animal's activity center increases, and λ_0 , the basal encounter rate, which indicates the expected encounter rate when the distance between the animal activity center and detector is zero (Efford, 2011; Goswami et al., 2019).

The data was organised as the actual geographical locations of adult male elephant detections from the field, and a separate “trap file” consisted of the geographical locations of the vertices of the 25 km² square polygons used for this study. Encounter histories were arranged using a standard SECR polygon search matrix consisting of the individual elephant sighting occasions, age, group type and group size were used as detection covariates. A state space of 1211 km²

was defined, including the study area and a 5 km buffer around it. Non-habitat areas within the state space, such as parts of Haridwar and Rishikesh, were removed. I hypothesised that λ_0 and σ would vary based on individual variations like age, group type and group size and modelled these as covariates. I ran 9 models (Table 3) and evaluated their fit to the data using maximum likelihood in package “secr.” (Efford, 2022) and selected the best model based on AIC (Akaike, 1974). Subsequently, I used the “region.N” function in package “secr” to derive the abundance for the specific area of interest (study area).

2.3.2 Association patterns

To check if there was a significant difference in the occurrence of different age classes across the three group types, I used a chi-squared test for independence.

The demographic composition of group types and the proportion of different age classes in group types were calculated. Multinomial regression was used to analyse the data collected on the association pattern of males as the response variable comprised three independent categories namely- All-male groups (AMG), mixed-sex herds and solitary. Each male elephant was considered a separate entry in the dataset with its associated covariates. I ran multiple models with different combinations of the predictor variables- Age, Body condition score, Physiological condition and Habitat type and then selected the best-fit model based on AIC. (Akaike, 1974) and residual deviance.

For multinomial regression, a category from the dependent variable is chosen as a reference, and then the odds of each of the other categories are calculated based on this reference. The model provides regression coefficients and the corresponding log odds, which can be exponentiated to give the odds ratios. Odds ratios for categorical predictor variables, like the ones in this study, compare the odds of each event (in this case, type of association) occurring

for each predictor category relative to the reference category, given that all other variables remain constant.

p-values were then computed for each category of the predictor variable to check which categories had a significant effect.

3. RESULTS

From 124 independent elephant sightings, 706 elephants were seen cumulatively. The proportion of elephants encountered under each age class was calculated (as shown in Fig 4).

Herds were encountered the most (50.8%, n=63), followed by solitary bulls (29.83%, n=37) and all-male groups (19.35%, n=24). The sex ratio of adult males to adult females was estimated at 1: 2.03. A ratio of adult makhna (tuskless male) to tusker was estimated to be 1:4.6 from the repository of identified males. For males, we followed the age classification specified in Table 2. The age structure of males expressed as the proportion of individuals classified across different age classes in the male segment of the population is presented in Fig. 5.

3.1 Abundance estimation

From a total of 77 detections for adult males, I identified 34 adult males with a sampling effort of 3014 km of search and 263 hours within three months. The SECR model space of a 5 km buffer included 1211 sq. km of elephant habitat. I ran 9 models, modelling λ_0 and σ as functions of three covariates – age class of the adult, group type and group size. The best model estimated adult male elephant density at 0.05 (SE 0.01)/ km² ($\lambda_0 \sim 1$, $\sigma \sim$ Group size). Subsequently, the abundance of adult males in the study area of 475 km² was estimated to be 40 (SE 1.4). The probability of detecting males within grids containing their activity centres (λ_0) was 28%. The value of σ , when modelled as a function of group size, was 4211.7 m or 4.2 km.

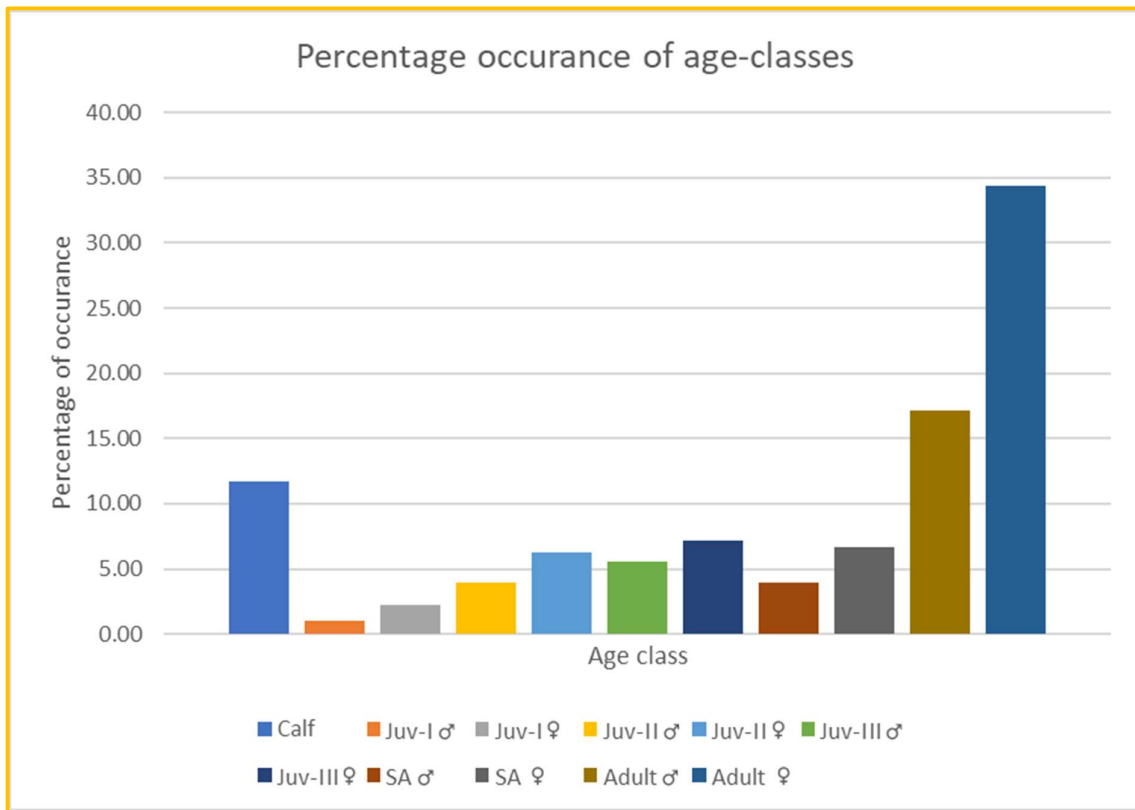


Fig 4 : Percentage of elephants seen in each age class expressed as percentages. Adult females represent almost 35% of the population.

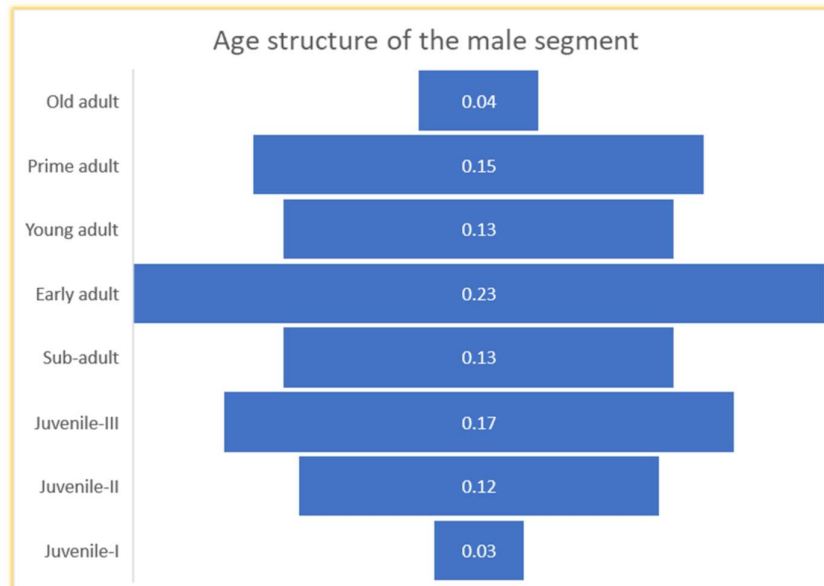


Fig 5 : Age structure of male elephants observed during the study. Early adults make up most of the male segment

Model	AIC	λ_0	σ (m)	Density (per sq km)
$\lambda_0 \sim 1$ $\sigma \sim \text{Group_size}$	3326.10 3	0.29 (SE 0.05)	4211.69 (SE 444.22)	0.05 (SE 0.01)
$\lambda_0 \sim \text{Group_size}$ $\sigma \sim \text{Group_size}$	3328.08 4	0.29 (SE 0.05)	4232.15 (SE 450.89)	0.05 (SE 0.01)
$\lambda_0 \sim \text{Group_size}$ $\sigma \sim 1$	3328.94	0.29 (SE 0.05)	4219 (SE 451.10)	0.053 (SE 0.01)
$\lambda_0 \sim 1$, $\sigma \sim 1$	3329.28	0.29 (SE 0.05)	4257.23 (SE 483.6)	0.05 (0.009)
$\lambda_0 \sim \text{Group_type}$, $\sigma \sim 1$	3329.55 8	0.38 (SE 0.08)	4239.26 (SE 461.21)	0.05 (0.01)
$\lambda_0 \sim 1$, $\sigma \sim \text{Adult_age}$	3330.02 5	0.28 (SE 0.04)	4798.66 (SE 857.17)	0.052 (SE 0.01)
$\lambda_0 \sim \text{Adult_age}$, $\sigma \sim \text{Adult_age}$	3330.39 5	0.23 (SE 0.06)	4562.99 (SE 537.57)	0.055 (SE 0.01)
$\lambda_0 \sim \text{Adult_age}$, $\sigma \sim 1$	3331.64 8	0.22 (SE 0.06)	4240.24 (SE 484.33)	0.054 (SE 0.01)
$\lambda_0 \sim 1$, $\sigma \sim \text{Group_type}$	3331.79 3	0.29 (SE 0.04)	4126.46 (SE 450.82)	0.05 (SE 0.009)
$\lambda_0 \sim \text{Group_type}$, $\sigma \sim \text{Group_type}$	3332.79 9	0.39 (SE 0.09)	4353.79 (SE 506.77)	0.05 (SE 0.01)

Table 3 : Model selection table for density estimation ranked by AIC. Model with σ as a function of group size had the best fit

3.2 Association pattern

Male elephants in the study area were seen in mixed-sex herds, with all-male groups, and as solitary individuals. The associations ranged from 1 to 47 individuals. The mean size of mixed-sex herds was 9.41 (SE 1.09, n=63, range=2-47). The mean size of all-male groups was 3.37 (SE 0.48, n=24, range =2-11). The proportion of different age classes of males in group types are given in Table 4.

Note: For ease of interpretation, age classes Juv-I, Juv-II and Juv-III have been represented as single-age class (Juv).

Juvenile and sub-adult males were primarily seen in herds, while Early adult males were seen in higher proportions in all-male groups. Old adults were seen in equal proportions in herds and as solitary. A chi-squared test of independence showed a significant difference ($X^2 = 107.19$, $df = 10$, $p\text{-value} < 0.05$) in the occurrence of the different age classes across the three different group types.

A body condition score (BCS) was assigned to each male encountered. Scoring ranged from 1 to 10. Most males were assigned BCS between 6 and 8, with no male scoring less than 5. Fig.6 shows the body condition scores of males across group types. BCS did not vary much across group types.

	All-male Group	Herd	Solitary
Juvenile	0.099	0.887	0.014
Sub-adult	0.214	0.679	0.107
Early Adult	0.660	0.120	0.220
Young Adult	0.536	0.179	0.286
Prime Adult	0.455	0.182	0.364
Old Adult	0.556	0.222	0.222

Table 4: Proportion of males of different age classes in different group types

	Juvenile	Sub-adult	Early Adult	Young Adult	Prime Adult	Old Adult
All-male group	8.64	7.4	40.7	18.5	18.5	6.1
Herd	62.3	18.8	5.9	4.95	5.9	1.98
Solitary	2.7	8.1	29.7	21.6	32.4	5.4

Table 5: Demographic composition of males (Percentage)in group types

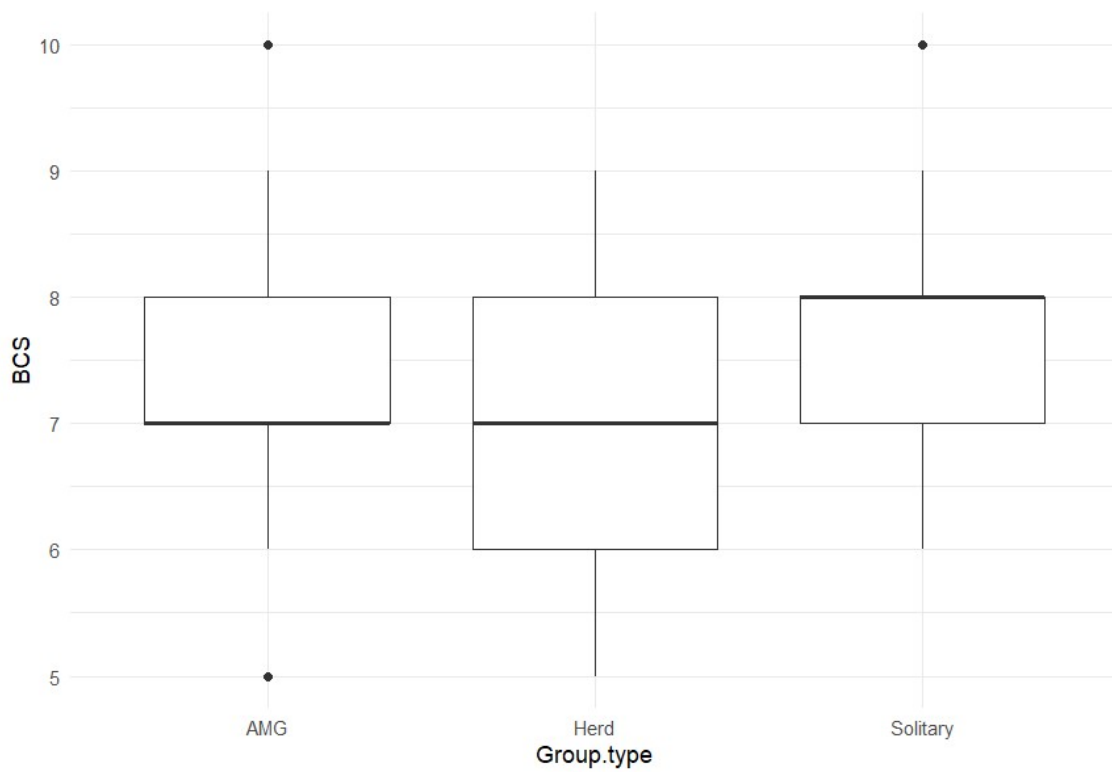


Fig 6: Box plots representing Body condition scores for males across group types

For the regression model, group type (All-male group, Herd or Solitary) was the response variable, with predictor variables being i) age – six age classes (Juvenile, Sub-adult male, Early adult, Young adult, Prime adult, and Old adult), ii) Body condition score, iii) Habitat type and iv) Physiological condition. Table 5. shows all the models used and how they are arranged based on AICc.

The model with the lowest AICc and residual deviance was selected from the model selection table. The model with Age, Habitat type, and Physiological condition as predictor variables was selected. A pseudo-R square value of 0.454 was also calculated, showing that the model has a good fit.

With 'Herd' as the reference category for the multinomial regression, coefficients for different categories of each variable were computed. Then, odds ratios for each category of the three variables were calculated by exponentiating the coefficients (Given in Table 6).

Model no	Intercept	Age	Body Condition Score	Habitat type	Physiological condition	df	logLik	AICc	delta	weight
14	+	+		+	+	24	-122.551	299.3	0	0.882
16	+	+	+	+	+	26	-121.999	303.3	4.02	0.118
6	+	+		+		22	-134.621	318.4	19.12	0
8	+	+	+	+		24	-134.076	322.3	23.05	0
10	+	+			+	14	-147.428	324.9	25.63	0
12	+	+	+		+	16	-146.664	328	28.73	0
2	+	+				12	-165.559	356.6	57.35	0
4	+	+	+			14	-164.889	359.8	60.35	0
7	+		+	+		14	-172.158	374.4	75.09	0
15	+		+	+	+	16	-170.442	375.6	76.29	0
5	+			+		12	-178.358	382.2	82.94	0
13	+			+	+	14	-176.283	382.6	83.34	0
11	+		+		+	6	-214.366	441.1	141.8	0
3	+		+			4	-218.303	444.8	145.5	0
9	+				+	4	-220.745	449.7	150.4	0
1	+					2	-224.525	453.1	153.8	0

Table 6 : Model selection table for multinomial regression. The combination of Age, Body condition score and Physiological condition was the best model.

	AMG	Solitary
Intercept	1.65E-09	6.57E-02
Juv	0.013861	0.003746
OA	8.56926	6.280008
PA	2.944643	5.35471
SAM	0.044657	0.050266
YA	0.847734	1.340303
Non-musth	53.33149	23.22585
Grassland	1.52E+08	1.41E+00
Moderately dense forest	12.53254	5.117745
Non-forest	3.80E+08	1.29E+01
Open	4.51E+07	2.36E+00
Scrub	3.30E+08	1.90E+00

Table 7: Odds-ratios for the selected model

<i>Predictors</i>	<i>Odds Ratios</i>	Group_type		<i>Response</i>
		<i>CI</i>	<i>p</i>	
(Intercept)	0.00	0.00 – 0.00	<0.001	1
Age [Juv]	0.01	0.00 – 0.06	<0.001	1
Age [OA]	8.57	0.55 – 132.48	0.123	1
Age [PA]	2.94	0.34 – 25.19	0.322	1
Age [SAM]	0.04	0.01 – 0.22	<0.001	1
Age [YA]	0.85	0.14 – 5.14	0.857	1
Physiological condition [Non-musth]	53.33	7.91 – 359.78	<0.001	1
Habitat type [Grassland]	151803921.79	64908628.82 – 355028770.31	<0.001	1
Habitat type [Moderately dense forest]	12.53	12.53 – 12.53	<0.001	1
Habitat type [Non-forest]	379722506.34	68717217.13 – 2098297746.18	<0.001	1
Habitat type [Open]	45143456.38	16906757.02 – 120539477.27	<0.001	1
Habitat type [Scrub]	329650773.99	118414251.99 – 917707378.70	<0.001	1
(Intercept)	0.07	0.01 – 0.78	0.032	3
Age [Juv]	0.00	0.00 – 0.04	<0.001	3
Age [OA]	6.28	0.38 – 103.27	0.197	3
Age [PA]	5.35	0.64 – 44.89	0.121	3
Age [SAM]	0.05	0.01 – 0.30	0.001	3
Age [YA]	1.34	0.22 – 8.34	0.752	3
Physiological condition [Non-musth]	23.23	3.47 – 155.27	0.001	3
Habitat type [Grassland]	1.41	0.19 – 10.30	0.731	3
Habitat type [Moderately dense forest]	5.12	0.62 – 42.10	0.128	3
Habitat type [Non-forest]	12.91	0.87 – 191.35	0.063	3
Habitat type [Open]	2.36	0.36 – 15.52	0.370	3
Habitat type [Scrub]	1.90	0.22 – 16.72	0.561	3
Observations	219			
R ² / R ² adjusted	0.454 / 0.450			

Table 8: Odds ratios, confidence intervals and p-values for all variables of the best model. Significant variables are in bold. Pseudo R² value is also given. Response 1 refers to AMG and Response 3 refers to Solitary.

After calculating the p-value, it was found that categories Juv, SAM, Non-musth, Grassland, Moderately dense forest, Non-forest, Open and Scrub were significant predictors ($p < 0.05$) for group type all-male group and similarly, categories Juv, SAM, and Non-musth were significant predictors ($p < 0.05$) for group type Solitary.

For Group type -All-male group

- The odds of a male being in an all-male group is reduced by a factor of 0.014 if the male is a juvenile compared to an Early adult (reference category for predictor -Age).
- The odds of a male being in an all-male group is reduced by a factor of 0.044 if the male is a sub-adult compared to an Early adult.
- The odds of a male being in an all-male group increases by a factor of 53 when the male is in non-musth compared to when in musth.
- The odds of a male being in an all-male group in Grassland, Non-forest, Open and Scrub are extremely high as compared to dense forest

For Group type Solitary

- The odds of a male being solitary is almost nil if the male is a juvenile compared to an Early adult.
- The odds of a male being solitary is reduced by a factor of 0.05 if the male is a sub-adult when compared an Early adult.
- The odds of a male being solitary increases by a factor of 23 when the male is in non-musth compared to when in musth.

From the results, we can interpret that juvenile males are more likely to be associated with a herd than with an all-male group but are more likely to join an all-male group than be solitary.

A similar case can be seen with sub-adult males. Adult males- those capable of coming into musth are more likely to be associated with a herd than with an all-male group when in musth. Certain habitat types also seem to be associated with a particular group type. Male elephants are highly likely to be seen in all-male groups in habitats like non-forest areas such as roads and near human habitation, open forests, grasslands, and scrubs. Herds tend to stick to areas with good forest cover.

4. DISCUSSION

The adult male to adult female sex ratio of 1:2.03 reported in the study is comparable to the 1:1.87 reported by Williams (2002) in western Rajaji. Results further indicate that the highly favourable male sex ratio remains unchanged since early 2000s. The adult sex ratio reported in the study is one of the least skewed among Indian populations and is comparable to the ones reported from certain high density populations such as Kaziranga in North-East India and Sri Lanka (De Silva, Ranjeewa, & Weerakoon, 2011; Goswami et al., 2019; Katugaha et al., 1999). For the male segment, young individuals (< 20 yrs.) made up almost 68% of the male segment, consistent with earlier findings from the landscape (Williams, 2002). Since the other metrics for population demography were not calculated, we can only assume that such a high proportion of young individuals in the male segment points towards high recruitment rates and low rates of juvenile mortality. This is worth detailed assessment by monitoring the population over time.

4.1 Abundance estimation for adult males

Spatially explicit capture-recapture (SECR) is a robust and powerful tool to estimate population sizes. Goswami et al. (2019) demonstrated the suitability of such methods to monitor Asian elephant populations reliably. Subsequently, camera trap-based SECR has also been used to assess the population size and structure of Asian elephants (Sun et al., 2021). In this study, polygon search-based spatially explicit capture-recapture (Efford, 2011) was used to estimate the abundance of the adult male segment of the elephant population in the eastern part of Rajaji National Park and adjoining areas. A combination of morphological characters was used to uniquely identify each individual. The ability to identify individuals can play a major role in

conservation since long-term monitoring of known individuals is essential for obtaining data on life history traits (Caro, 1998).

The results indicate that the movement parameter/ spatial scale of detection σ is influenced by the group size. The positive beta coefficient also shows that σ increases with group size, demonstrating that adult males when in larger groups, like in mixed-sex herds, have greater space use and movement about their activity centres as compared to when in smaller groups or when solitary. Larger home range sizes in males are often associated with *musth* - a period of heightened sexuality and aggression (Chelliah & Sukumar, 2013; Goswami et al., 2019; Sukumar, 2003). When in musth, males may adopt a roving strategy in order to find potential mates (Fernando et al., 2008; Keerthipriya et al., 2020), leading them to move around more and cover larger areas. For the study period, only a small proportion of males, eight out of 34 identified, were seen in musth. From the results, it can be cautiously interpreted that musth may not have as much influence on the movement in this landscape possibly due to limited elephant range, and relatively high density of males in the population. It is also possible that when in smaller groups or solitary, males are more localized in their space use. This also points to the fact that larger groups are easily detectable over larger distances. While I hypothesised that age and group type may play a role in determining detection probability of bulls, their specific covariates did not receive adequate support in the models used. The model with σ as a function of group size had received good support from the data with low standard error and narrow confidence intervals.

Nonetheless, it is known that animals do not move randomly throughout areas and, indeed, have highly structured movements influenced by the landscape (Marrotte et al., 2022).

Human settlements (Van Gujjar community) are interspersed throughout the study area, even within forested areas, which may affect the manner in which individuals utilize the landscape.

Since I did not have any specific landscape covariate to model with, other individual covariates were used.

The results from this study not only highlight the effectiveness of SECR models in accurately estimating elephant densities and abundance as demonstrated in previous studies (Goswami et al., 2019; Sun et al., 2021) but also present polygon search as an effective field method entailing capture-recapture studies for Asian elephant populations.

The Rajaji landscape is an essential area for Asian elephant conservation and, together with the Lansdowne Forest Division and Corbett Tiger Reserve, forms an important habitat vital for the continued existence of the North-western elephant population in India. If robust methods such as SECR can be applied to this larger landscape, we can obtain near-accurate estimates of the male segment and the entire population. These numbers can better inform management practices and help conserve this crucial landscape and its functional role in sustaining elephant and other wildlife habitats and populations.

4.2 Factors affecting association patterns of male elephants

The results of the present study show that a combination of age, physiological condition, and habitat type best explained the male association patterns. Body condition score was not a significant predictor of group type association, possibly due to scores not showing much variation across group types and age-classes. While only juvenile and sub-adult male age-classes were significant, with higher odds of associating with herds, different group types showed clear habitat associations and non-musth males has higher odds of associating with all-male groups.

Elephants may form associations for various reasons, including networking, bonding, mating, resource acquisition, and protection against predators and poaching (Sukumar, 2003). For male associations, the type of association or group type may also relate to certain life history strategies as I discuss below. Asian elephants are capable of infrasonic communication (Payne et al., 1986). For this study however, I had no means of ascertaining whether such communication routes were used. Therefore, the assigning of group type was merely based on the spatial distribution of animals. I along with my team of three field assistants spent almost 263 hours tracking, following and observing elephants as I also collected behavioural data. This ensured that the correct group type was assigned to each individual, particularly solitary individuals as we could visually confirm that these males were not in proximity to other males.

4.2.1 Influence of age

Male elephants have distinct periods in their life associated with different life-history strategies (Lee et al., 2011; Sukumar, 2003). The study found that the occurrence of different age classes significantly differed across group types, with juveniles and sub-adults mostly seen with mixed-sex herds. Older males (adults) were hypothesized to be primarily associated with all-male groups. While the hypothesis holds true, age alone does not determine the group type association. Physiological condition and habitat also play a significant role.

Juvenile and sub-adult males were highly likely to be seen with mixed-sex herds but were more likely to be seen with all-male groups than remain solitary. These findings could be the result of the need for younger males to learn socially as well as for protection. Younger males are also known to stay with the natal group till adolescence.

Early adults (15-20 years) were mostly seen in all-male group, making up 40% of the demographic composition of all-male groups. These results are consistent with previous studies

on African and Asian elephants (Chiyo et al., 2011; Srinivasaiah et al., 2019). Testing strengths by sparring with age peers was hypothesised to be the reasons for this pattern. While only association data cannot be used to confirm the same with respect to this study, field observations and preliminary data on behavioural interactions do seem to point in the same direction.

4.2.3 Physiological condition

Physiological condition also influenced group type membership. Non-musth males had higher odds of being in all-male groups compared to being in herds. The finding that males in musth are seen mostly with mixed-sex herds corroborates the same by La Due et al. (2021). Non-musth males were seen more frequently with all-male groups with age, and older males (>30 yrs) were also regularly seen with all-male groups. It was mostly older males (Prime adults and Old adults) that were found in musth. When in musth, males the frequency of adult males associated with mixed-sex herds increased significantly. The physiological and behavioural changes male undergoes during musth are designed to increase its mating success (Sukumar, 2003). Therefore, it is only natural for musth-males to associate exclusively with mixed-herds during this period. Whether or not this translates directly into increased mating success is not known. Observations indicate that once the older bulls entered musth and associated more with mixed-sex herds in search of oestrus females to mate with, the frequency of all-male groups crossing the Ganga reduced, and the so did the size of all-male groups, hinting at possible leadership roles of older bulls (Allen et al., 2020; McComb et al., 2011).

Despite the hypothesis that younger males (Early adults) would associate more with herds for opportunistic matings, the high frequency of early adult male association with all-male groups and non-musth males being mostly associated with all-male groups proves this hypothesis

incorrect. Body condition did not play a significant role in explaining association patterns, likely because of low variation in the scores among males.

4.2.3 Habitat type

Habitat type emerged as a significant predictor influencing male associations, especially for all-male groups compared to mixed-sex herds. The results indicated that the odds of all-male groups being in grassland and non-forest areas were particularly high. This is in line with the findings of Srinivasaiah et al. (2019), who found that forest contiguity was the main factor determining the formation of all-male groups, with all-male groups almost exclusively forming in fragmented landscapes.

All male groups in the study were seen in areas near human habitation and were actively involved in crop raiding, similar to their African counterparts (Chiyo et al., 2012). In Rajaji, only males, solitary or in all-male groups, are known to cross the Ganga from the eastern side to the western for crop raiding (Nigam et al., 2022). Females doing the same has not been reported from this region. Interestingly, there were instances where a juvenile was observed associating exclusively with all-male groups in open habitats and settled areas, as well as crossing the Ganga in the evening along with the older males to crop-raid on the other side and returning the next morning. This tallies with the results that state that males seen in open habitats such as grasslands, non-forest areas and scrubs, are highly likely to be seen with all-male groups. This is in line with the findings of Srinivasaiah et al. (2019) that such male associations are environmental rather than biological.

There were some instances wherein prime adult and old adult males were seen to cross the Ganga and crop raid solitarily. Since these all-male groups are associated with a higher tendency to perform the risk-prone activity of crop-raiding, the “dilution effect hypothesis” may provide an explanation. The hypothesis states that being in larger groups dilutes/reduces the individual risk (Hammer et al., 2023; Ydenberg & Dill, 1986) here, the risk is conflict with humans. More studies on all-male groups and the risk of human-elephant conflict are required to confirm this.

Srinivasaiah et al. (2019) provided evidence that all-male groups in human-modified environments represent an adaptive strategy. This study also supports this by showing that all-male groups were largely restricted to being near human habitation. Detailed behavioural observation of stable all-male groups is necessary to fully elucidate the various factors affecting group formation. Such research is important for understanding the social organization of male elephants and human-elephant interactions. In addition, an analysis of crop-raiding patterns of all-male groups may help identify targeted solutions for conflict mitigation, as well as guide the development of evidence-based recommendations for long-term conflict management.

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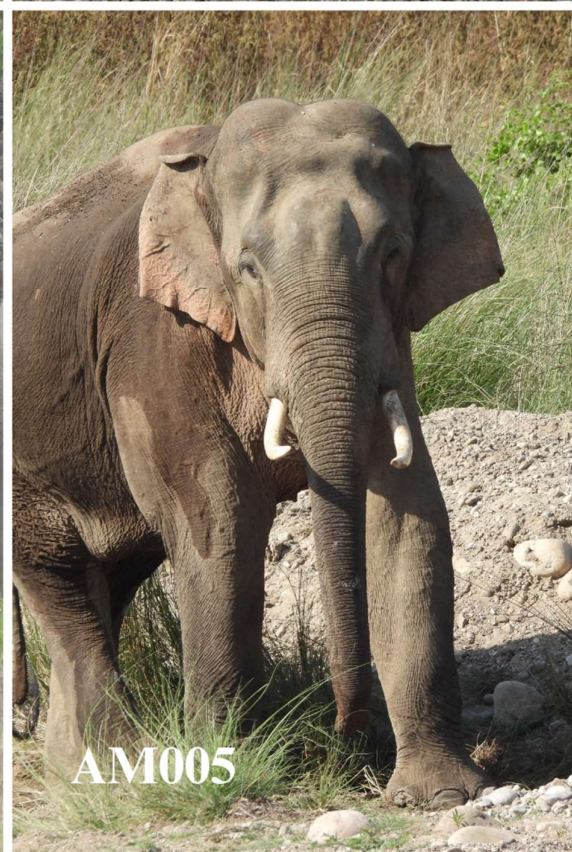
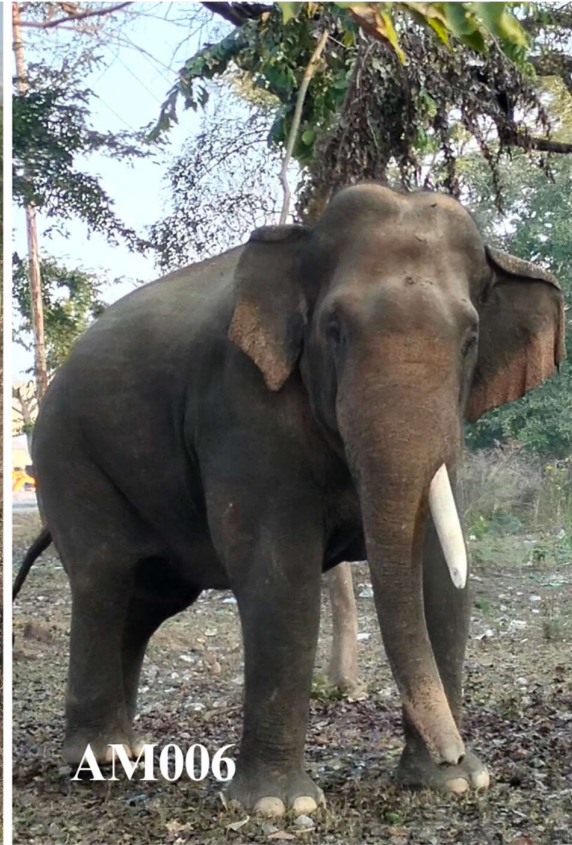
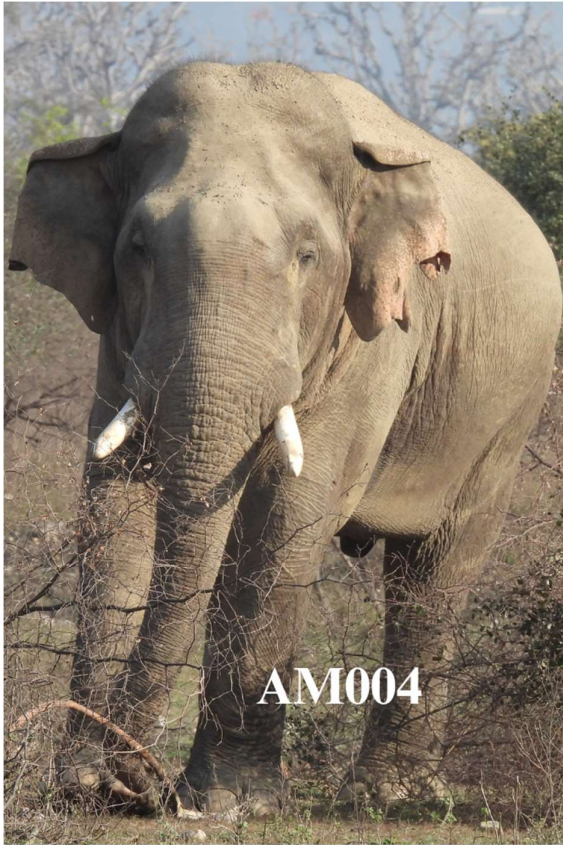
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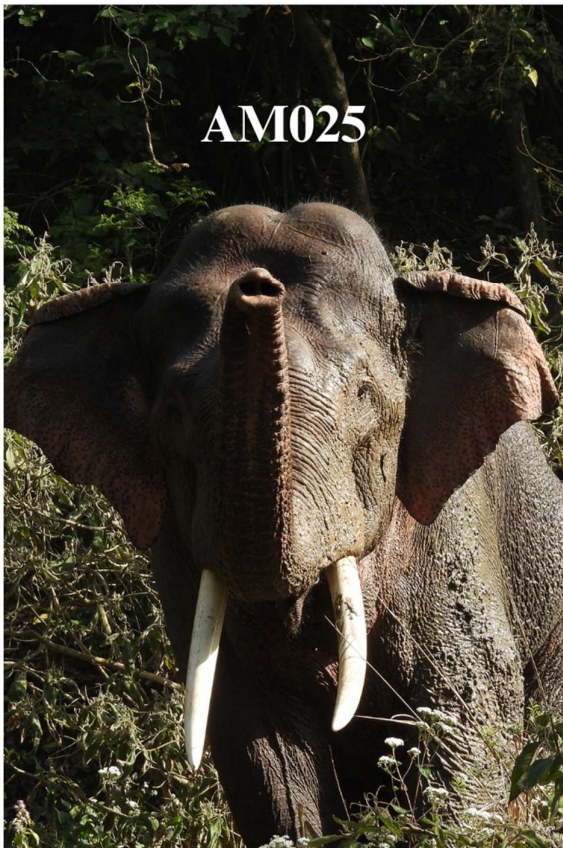
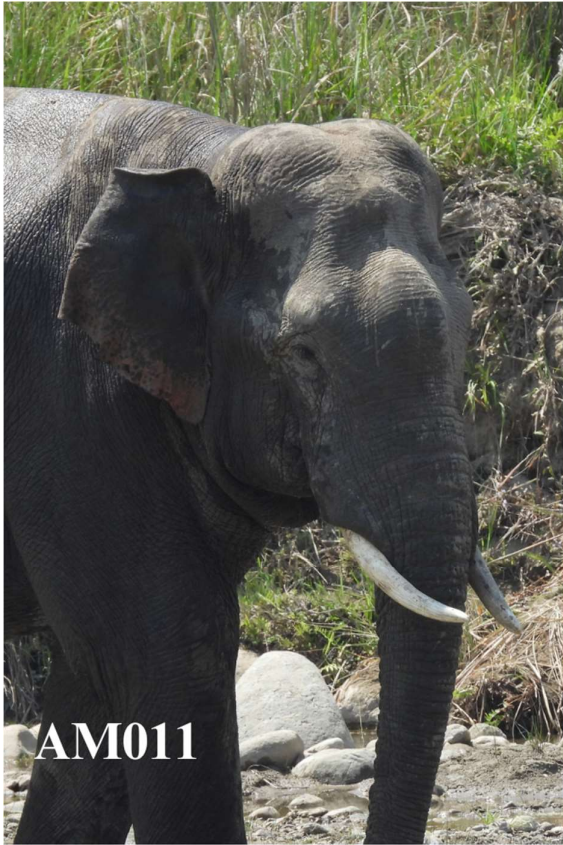
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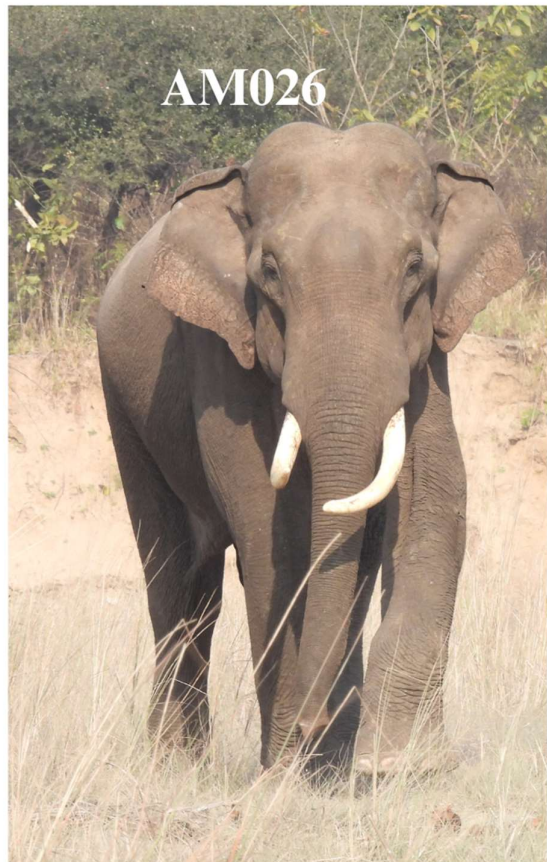
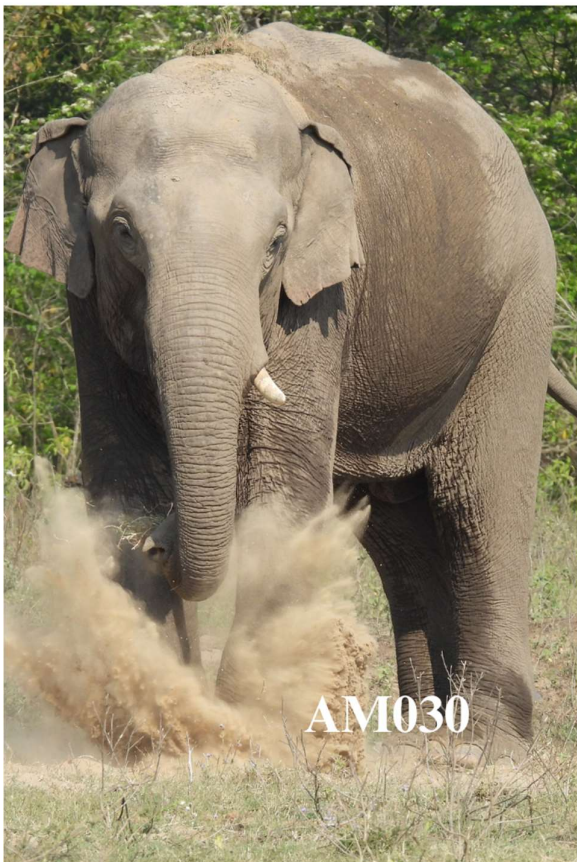
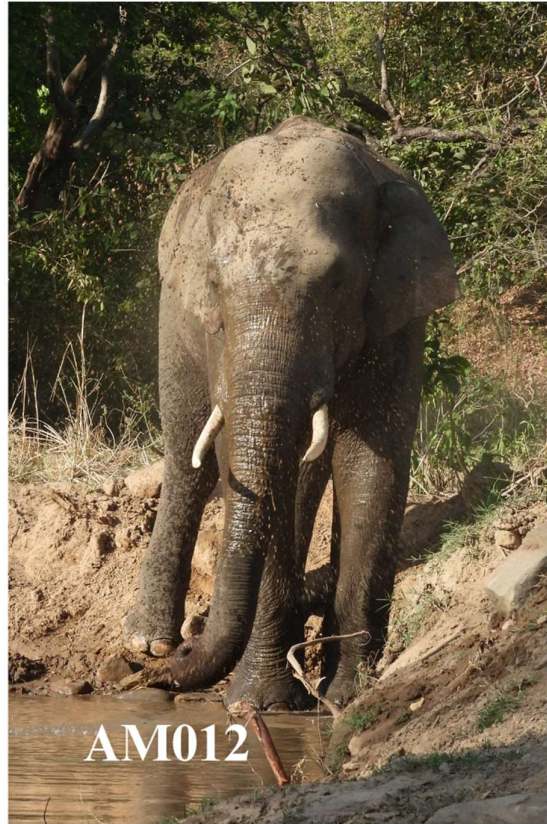
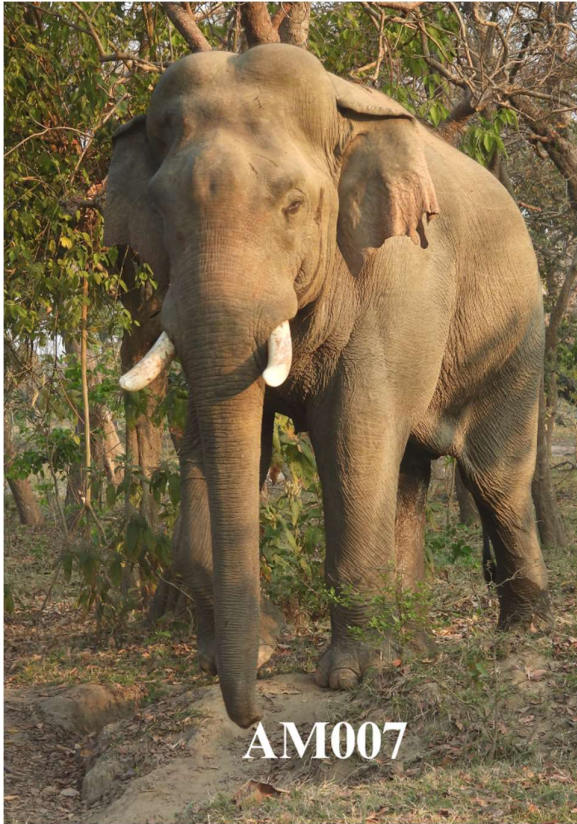
APPENDICES

Appendix 1 : Photographs of select adult males from Rajaji National Park and Haridwar Forest Division









Appendix 3 : Pictures representative of the three group types – adult male with a mixed-sex herd, an all-male group of three adult males and a solitary adult male.

